FOREST TREE PHYSIOLOGY SYMPOSIUM

FOREWORD

In addition to holding numerous special days and events, it was felt that to hold several scientific symposia during the Diamond Jubilee Year of the Ohio Agricultural Experiment Station would be a fitting way to commemorate the great contributions to science made by members of the staff during the institution's 75-year history.

The Forest Tree Physiology Symposium, held on June 13 and 14, 1957, was symbolic of this recognition. Forestry has been an important segment of the Experiment Station's program from the beginning. The late Edmund Secrest, director of the Station from 1937 to 1947, was a forester and it was only natural for him, in his capacity as head of the Forestry Department and as State Forester, to develop this program on a state and national basis.

More recently, as technology and basic knowledge more closely merged, the need for greater emphasis on basic research for yielding new knowledge on which to build an even stronger technology became apparent and was encouraged. This is reflected in the current forestry research program and in the contributions made by members of the Forestry Department staff to this symposium.

Represented in attendance at the symposium were three foreign countries and fifteen states. The presence of foresters, physiologists, plant pathologists, entomologists, botanists, and agronomists attested to the broad interest of overlapping fields and typified the modern basic scientific approach to the solution of our practical problems.

To those whose responsibility it was to prepare the program, to those who made such noteworthy contributions to the program, to those sponsors whose contributions helped make the symposium possible, and to The Ohio Journal of Science for publication of the proceedings, our deepest appreciation is herewith extended.

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RECENT TRENDS IN PLANT PHYSIOLOGY[1]

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It is a privilege to be the first to have the floor in this "Forestry Physiology Symposium," and I wish to start by paying a brief tribute to the background of circumstances which has prompted this occasion. This year marks the 75th anniversary of the establishment of the Ohio Agricultural Experiment Station and this symposium represents one of the special events which has been planned in recognition of this fact. It seems especially fitting that a program in forestry should be one feature of this anniversary year, since forestry has long occupied a prominent place in the program of the Ohio Agricultural Experiment Station. The Secrest Arboretum, to mention only one aspect of the forestry program, is now, and long has been, a distinctive and valuable feature of this institution.

The topic on which I have been asked to speak is that of "Recent Trends in Plant Physiology." I presume that the objective of my remarks should be to provide a generalized backdrop of ideas for the presumably meatier intellectual fare which is to follow. In one way this is an easy topic to speak on; its very breadth gives me plenty of leeway. In another way it is a very difficult topic, because the problem of setting its boundaries is left completely in my hands. For example, what construction shall I put on the word "recent"? This is an elastic word but I am not going to stretch it too far; the pertinence of my remarks will extend backwards in time for not more than ten, or at the most, fifteen years.

I propose to discuss this topic under four main categories: (1) trends in points of view, (2) trends in research emphasis, (3) trends in experimental techniques, and (4) trends in the kinds of plants used for experimentation.

The most pronounced change in the approach to many phases of plant physiology in recent years has been the shift from a chemical to a biochemical viewpoint. Even the chemical approach to plant physiology, in any comprehensive sense of the word, does not date back much further than the beginning of the present century. Prior to that time much emphasis was placed on the so-called stimulus-response physiology, with no very serious attempts to probe internally into the accompanying processes.

Toward the close of the Nineteenth Century, chemistry first began to achieve real stature as a science. Under the impact of a wave of important discoveries, supported by brilliant theoretical interpretations, by such men as Arrhenius, vant Hoff, Perkin, Gibbs, Ostwald, Raoult, Freundlich, and Kekulé, chemistry became the most respected of all sciences. At this period all of these stars, and many others, shone so brilliantly in the chemical heavens that all of science was illuminated. The new era in physics was not to dawn for another quarter of a century.

The many significant advances made in chemistry during the late Nineteenth and early Twentieth centuries led to a marked increase in attempts to interpret physiological processes in terms of chemical principles. Many plant processes were investigated and interpreted from this viewpoint, but one example will suffice for the present discussion. The well known formaldehyde theory of photosynthesis, first suggested by Baeyer in 1870, was still being supported by investigators of note as late as the early thirties. Anyone who is even casually familiar with current literature on the mechanism of photosynthesis realizes how widely

the long respectable formaldehyde theory fell wide of the mark, yet from the purely chemical viewpoint, it was a perfectly valid and plausible hypothesis. Not all interpretations of plant physiological processes from the viewpoint of chemistry during this period proved as inadequate as the example given. By and large, however, the results of probing into the nature of physiological mechanisms from this viewpoint did not prove as fruitful as many investigators of that period had hoped.

Although there is a very real difference between the two, it is difficult to put into exact words the distinction between a chemical and a biochemical viewpoint. The former might be described as that of test tube chemistry. But the reactions of living organisms do not occur in test tubes. Neither can they be wholly explained by the principles of test tube chemistry. In biochemistry reactions a straight line is not necessarily the shortest distance between two points. From the viewpoint of the conventionally-minded chemist, the reactions which occur in living organisms appear devious and circumlocutory. This does not mean, of course, that the recognized principles of chemistry have been repealed in the biochemical world. Rather it means that these same principles are at work in systems which rarely, if ever, exist outside of living organisms, and it is this different framework of operation which gives to biochemical reactions their distinctive aspects.

One example may serve to illustrate and clarify the immediately foregoing remarks. The late William Lloyd Evans, longtime and well-known professor of chemistry at The Ohio State University, was a recognized authority on carbohydrate chemistry about a generation ago. Among other carbohydrate problems which he studied was that of their stepwise degradation under various conditions. Dr. Evans succeeded in working out the sequences of reactions involved in such breakdowns of carbohydrates in great detail. But it was noteworthy that, in the inanimate systems with which he was dealing, such degradative reactions only occured in the presence of a strong acid, or a strong alkali, and that high temperatures were also often required. I remember discussing with Dr. Evans on several occasions what possible light his findings could throw on the degradation of carbohydrates in living cells. The problem was not illuminated by his work because strong acids, strong alkalies, or high temperatures do not exist in living cells.

Actually, as of today, not much more than twenty-five years later, the stepwise degradation of the carbohydrates is one of the most thoroughly understood aspects of cellular metabolism. The process as it occurs in living cells does not remotely resemble what went on in Dr. Evans' test tubes. It has been investigated in mammalian tissues, in microorganisms, and in the tissues of higher plants, and seems to be basically similar in all kinds of living cells. Even the beginnings of progress in elucidating this complex phenomenon were not made, however, until it was studied in relation to the compounds and systems actually present in living cells. Only in terms of enzymes and coenzymes, hydrogen acceptors and donors, phosphate acceptors and donors, and low and high energy bonds could this complex process be resolved into its component reactions. Counterparts to all these entities also exist in nonliving systems but seldom if ever in such complex arrays as they are found in living cells.

Let us now turn our attention to recent trends in research emphasis in the realm of plant physiology. Preeminent among these is the field of plant metabolism by which is meant all of the reactions and chains of reactions, forwards, backwards, sidewise and cyclical, occurring within the metabolic pool in the matrix of the protoplasm. More than in any other field advances in this phase of physiology have been dependent upon a biochemical foundation and the adoption of a biochemical viewpoint.

In recent years our knowledge of the metabolic pool in plants, with its numerous eddies, cross currents and whirlpools, has steadily become wider and deeper.

The metabolic pathways in the oxidation of carbohydrates, as previously indicated, are quite well understood. The biochemistry of photosynthesis, although not, parenthetically, its energetics, is approaching a comparable status of knowledge. Similarly, knowledge of the metabolism of organic acids, fats, and nitrogenous compounds has progressed substantially in the last decade or two. The general advance in our understanding of the overall dynamics of plant metabolism has been one of the most outstanding achievements of plant physiology during the last two decades.

Research in plant hormones is another field of investigational activity which has retained its prominence in recent years. Work on the auxins has continued at a steady pace and substantial progress has been made in understanding many of their properties except the most basic one of just what is their metabolic role in the plant cell. Plausible concepts have been worked out relating the structure of molecules to their effectiveness as auxins. The kinetics of auxin action have been studied and not unsurprisingly have been found to resemble the kinetics of enzymatic reactions. Rational explanations for the action of antiauxins in counteracting effects of auxins have been developed on the basis of a mechanism of competitive inhibition.

Work on other kinds of plant hormones besides the auxins has continued in recent years, and some entirely new ones have been discovered. Investigations have continued on the roles of thiamin, niacin, pyridoxine and other plant hormones of the B vitamin group. Probably much more epoch-making in its implications, however, is the recent discovery by a team of research workers at the University of Wisconsin of the cell-division promoting hormone called kinetin. The roles of this hormone and the probably other similar compounds in plants are still largely unexplored, but it seems likely that hormones of this type may be found to rank with the auxins in the universality of their effects.

And finally we must not overlook the latest cinderella of plant hormones, gibberellic acid. Although studies of this substance have scarcely advanced beyond the "spray it on and see what happens" stage, its introduction has been accompanied by such a flux of publicity that almost everyone has heard of it. There are more articles about gibberellic acid in popular journals than in scientific ones. Sometimes known as the "neck-stretching" hormone, because its most spectacular effect on plants is to promote the elongation of stems and other organs, gibberellic acid has also been reported to have many other effects on plants. Among these are the induction of flowering in certain species under conditions which otherwise do not induce flowering. Practically all work on this hormone to date has been of a preliminary nature and a true appraisal of its role in plant growth and metabolism must await further experimentation. Likewise, such practical applications as this substance may ultimately prove to have must await a better understanding of its basic physiological effects.

In the above paragraphs I have discussed hormones only in the narrower sense of compounds known to be endogenous synthetic products of plants. As is well known, many compounds not known to be natural plant metabolites have hormonelike effects on plants. Two-4 dichlorophenoxyacetic acid (2,4,D) and maleic hydrazide, to mention only two of the better known ones, are examples of compounds in this category. Most experiments on effects of nonendogenous hormones on plants have been empirical in approach and, in my judgment, will therefore not yield scientific profits of lasting benefit, either in their basic or applied aspects. A deeper insight into the roles played by such compounds in plant metabolism will give a sounder basis for judging their possible uses from more practical standpoints.

One other strong research trend in recent years which deserves mention has been an expanded interest in the photoreactions of plants. Although such long-favored lines of research as the action spectrum of photosynthesis and the quantum

efficiency of photosynthesis have not been entirely neglected, much of the work on photoreactions in recent years had its genesis in investigations on photoperiodism. Pioneer investigations on the action spectrum of the low energy light reaction of photoperiodism and certain other light-sensitive processes by Borthwick, Parker, Hendricks and their associates at Beltsville, Maryland, led to the discovery of the reversible red $\rightleftarrows$ far-red reaction in the physiology of plants.

The essence of this finding is that in various light-sensitive reactions a narrow band of wave lengths in the red with a peak at about 6600Å causes the reaction to go in one direction, while an adjacent band in the far-red with a peak at about 7350Å causes the same reaction to go in the opposite direction. In general, also, the reaction goes the same direction in the dark as under far-red irradiation, but at a much slower rate. Furthermore the reaction is reversible, often for an indefinite number of times. In light-sensitive lettuce seed for example, brief exposure of the seed to the red band of light greatly promotes its germination. If the exposure to the red band is followed shortly by a brief exposure to the far-red band, the promoting effect of the red light is mostly or entirely offset. A second exposure to red following the exposure to far-red has a promoting effect on germination, while a second exposure to far-red following the second exposure to red has an inhibiting effect. The reversibility of the reaction has been demonstrated to extend over a long series of alternations between irradiation with red and with far-red light.

The most amazing feature of this reversible reaction is the multiplicity of plant physiological phenomena and processes in which it appears to play a role. Among these are the photoperiodic reactions of both long and short day plants, the germination of light sensitive seeds, the elongation of coleoptiles, hypocotyls, and epicotyls, the expansion of leaf blades, the germination of fern spores, and the synthesis of flavone pigments. Other phenomena in which it is believed, although not as yet experimentally confirmed, that this distinctive light reaction may also play a role are anthocyanin formation, succulency, tillering, epinasty, bulb formation, tuberization, abscission, fasciation, cambial activity, and sexual expression.

The array of dissimilar processes in which this reaction appears to play a role is one of the most fascinating discoveries in all of botanical science in recent years. Unquestionably one of the master or key reactions in plant metabolism has been revealed by investigations in this field of photophysiology. In this respect this reversible photoreaction resembles the reaction catalyzed by auxin which is also obviously a key reaction in plants.

Let us now turn our attention to recent trends in the kinds of experimental techniques being used. I will mention first the employment of artificially controlled environments for physiological investigations with plants. Such artifically controlled environments usually take the form of small rooms in which at least the factors of light and temperature are controlled, and often others as well. Although earlier attempts to construct such facilities had been made, and temperature and humidity controlled dark rooms for auxin work date back about a quarter of a century, it was not until the advent of modern refrigeration engineering and of the fluorescent lamp that the development of such research facilities for plant physiological research became generally feasible. Ten years ago such controlled environment rooms were a rarity; today there is scarcely an institution pretending to do serious research on the physiology of plants which does not possess one or more.

Pioneer work on the development of such rooms was done by Parker and Borthwick of the U. S. Dept. of Agriculture and their light room at Beltsville was one of the first effective installations of its kind.

The most outstanding and well-known example of an installation for the growing of plants under controlled environments is the Earhart Plant Research Laboratory which was developed under the direction of Dr. Frits Went at the California Institute of Technology. This unique installation, often called the

"phytotron," comprises fifty-four separate units, many of which are air-conditioned greenhouses and darkrooms. There are thirteen rooms in which the factors of temperature, humidity, and light are all artificially controlled. In certain rooms still other factors such as wind velocity, rainfall, fog, and composition of the atmosphere are also controlled. The ionic environment of the roots and other substratum conditions are kept under control by growing all plants in gravel irrigated by suitable culture solutions. Special precautions are also taken to maintain, as nearly as possible, sterile conditions throughout the phytotron. Since Pasadena has been engulfed by the smog belt, it is probable that the only really healthy plants in town are those growing in the filtered air of the phytotron!

It should perhaps be emphasized that controlled conditions—at least in biological work—do not usually refer to constant conditions. Temperature and light, clearly the most significant of the environmental factors from the standpoint of most physiological processes, represent the irreducible minimum of factors which must be controlled if results of any significance are to be obtained. Temperature control is usually so arranged that dark period temperatures are lower than light period temperatures. Light is controlled with respect to length of the photoperiod, and, within limits, at least, in irradiance and quality. For many important types of physiological work with plants, control of no more than these two factors is adequate.

The obvious advantage of controlled climate rooms is that of reproducibility of experimental conditions from one experiment to the next. A group of plants can be exposed to the same environmental conditions in July, for example, as another group raised in January. Or, what is perhaps even more important, experiments conducted in one laboratory can be exactly duplicated in another laboratory. Furthermore, systematic variation of environmental factors from one experiment to the next can be accomplished in no other satisfactory manner than by the use of suitably equipped climate control rooms. Operation of a number of such rooms simultaneously obviously provides the most flexible facilities for such experimentation. Even when only one environment control room is available, however, such experiments can be performed, if the range of operation of that room is sufficiently flexible, by running the experiments in series.

The wide use in recent years of environment control rooms has led to immeasurable progress in increasing the accuracy of our knowledge of various growth reactions of many species of plants, especially to the factors of light and temperature. The almost spectacular advances in our knowledge of photoperiodism in plants in the last decade would scarcely have been possible without the employment of such facilities. Likewise knowledge of temperature effects on plants has been greatly advanced by such facilities.

A second widely used and potent new technique of physiological research has been made possible only by the advent of the modern alchemist who operates in the realm of physics rather than of chemistry. By unleashing powers only dreamed of yesterday he can, in the cyclotron and nuclear reactor, bring about the transmutation of one kind of atom into one of its isotopes, or even into an atom of an entirely different species. Many of these artificially produced isotopes are radioactive. That certain naturally occurring atoms such as radium, thorium, and uranium are radioactive has long been known, but it has been only for a comparatively few years that it has been possible to endow many of the physiologically important elements with the property of radioactivity. Some of the radioisotopes which have been most widely used in plant physiological research are Na^{24}, P^{32}, K^{42}, C^{11}, C^{14}, S^{35}, and Ca^{45}.

Such radioisotopes constantly betray their presence, wherever they may be, by the continuous emission of radiations or charged particles which can be detected by suitable instruments. If such radioisotopes are incorporated into molecules, it is often possible to trace their pathway through an organism, after absorption

or ingestion, and even to discover the chemical reactions in which they participate. This has never been possible by conventional methods of chemical analysis because by such methods it is impossible to distinguish between the introduced molecules and other molecules of the same species which were already present in the organism.

Some stable isotopes, of a mass unlike that of the most common isotope of the same element, have also been used as tracers in the investigations of various plant processes. The presence of such non-radioactive isotopes can be detected with a mass spectrograph. Several such isotopes which have been widely used in plant physiological research are H^2, O^{18}, C^{13}, and N^{15}.

So extensively have stable and radioactive isotopes been used in the investigation of plant physiological problems that it is difficult to realize that these techniques have been available for less than 20 years. Isotopes have been used as tracers especially in following the route of translocation of various kinds of solutes through plants and in the investigation of metabolic pathways.

The first critical demonstration that the upward movement of mineral salts absorbed from the soil occurred through the xylem of plants was made by the use of radioisotopes by Stout and Hoagland in 1939. Downward translocation routes have also been followed in similar fashion by introducing radioactive compounds into leaves, and many other aspects of the absorption and translocation of solutes are amenable to experimentation in which isotopes are employed as tracers.

The metabolic pathways in photosynthesis, respiration, amino acid synthesis and other similar processes have been explored extensively by isotope tracer techniques. When leaves, or algae, for example, are allowed to absorb carbon dioxide in which the carbon is isotopically distinctive, and the reaction stopped by killing samples of the tissue at various intervals after the start of the experiment, important clues as to the metabolic sequence of events can be obtained. The kinds of compounds into which the labelled carbon has been incorporated after different time intervals can often be ascertained. Chromatographic techniques, to which further reference will be made later, are often used in order to separate and identify the compounds into which the isotopically distinctive carbon has been incorporated. By a similar technique, the source of the oxygen liberated in photosynthesis has been shown to be largely, if not entirely, from the water molecules, rather than from the carbon dioxide molecules. By using alternatively water and carbon dioxide made with the O^{18} isotope of oxygen as raw materials in photosynthesis, it has been possible to make a decision regarding this basic fact in the mechanism of photosynthesis.

Although, strictly speaking, more of a biochemical than a physiological tool, no account of recent trends in techniques would be complete without some mention of paper chromatography. The use of this method is generally considered to have started with the work of Cosden, Gordon and Martin in 1944. Although other factors are also involved, the basic principle of paper chromatography is that of the partition of a solute between two immiscible liquid phases. The method is a micro one, as only very small quantities of test solution are used. It can be employed for the separation and subsequent identification of a number of the components in solution in a single sample.

A variety of paper chromotographic techniques have been developed, one of the most widely used of which is two-dimensional chromatography. The essentials of this method can be described in a few sentences. A piece of suitable filter paper is cut to suitable dimensions, a square piece 50 cm. on an edge being a representative size. A small drop of the test solution is applied near one corner of the paper and allowed to dry. Sometimes, in order to introduce a larger sample into the system, several drops are applied, each being allowed to dry before the next one is added. The paper is then suspended with its lower edge in the first liquid to be used until it has risen by capillarity almost to the top of the sheet.

The sheet is then dried, and resuspended in a second liquid whose front is at right angles to that of the first liquid. The first liquid used might, for example, be water-saturated phenol, the second α-picoline-water, but many other combinations are employed.

As a result of this procedure, for reasons too complex to enter into in this brief review, the various components of the sample become distributed on the paper according to a definite pattern, each, however, usually being restricted to a relatively small area. After such a separation has been achieved the position of the various spots on the chromatogram can be detected by various procedures, such as by color reactions, by autoradiography (for tagged compounds), by fluorescence or absorption in the ultraviolet range, or by microbiological reactions. The location of the spot in itself serves to identify or help identify the compound which it represents, but this can be followed by confirmatory qualitative tests, and often also by quantitative tests for the substance concentrated in any given area of the chromatogram.

The technique of paper chromatography has been applied to the micro-separation and microanalysis of virtually every known class of chemical compound from inorganic ions to some of the most complex known organic compounds. Its applications to problems in the biological sciences are legion. In the realm of plant physiology, for example, it has been used for the separation and identification of the intermediates of photosynthesis and other metabolic processes, for the identification of the individual amino acids occurring in plant tissues of various kinds, and for the separation of auxin and auxinlike compounds extracted from plant tissues.

I shall now speak briefly on trends in the kinds of plants used in experimentation. Algae have come increasingly into prominence as experimental organisms in recent years. *Chlorella*, first used as an experimental plant in photosynthetic work by Warburg nearly 40 years ago, is still a favorite. Several species and various strains of this alga have been employed. Other species of green algae such as *Chroococcus* and *Scenedesmus* have been used in various kinds of physiological work as have also a number of species of the blue green algae such as *Anabaena*, *Nostoc*, *Calothrix*, *Coccochloris*, *Periocystis* and *Diplocystis*. Recent work on the blue green algae has been stimulated by an increasing realization of the role of this group of organisms in nitrogen fixation.

Several reasons can be advanced for the increasing popularity of algae as laboratory test organisms. Many of them can be obtained in pure culture which is a definite advantage for certain types of research. Two universities in this country, Indiana University and the University of Georgia, have recently developed stock collections of hundreds of species and varieties of algae, mostly in pure cultures, from which subcultures can be obtained by interested investigators for physiological or other types of research. Such stock culture collections of bacteria and fungi have long been in existence, but establishment of such collections of algal cultures is, for this country, an innovation, although Cambridge University in England has long possessed one.

The obvious convenience of working with small samples which nevertheless represent thousands of individual organisms has endeared the algae to many investigators, especially those working on such fundamental problems as the mechanism of photosynthesis. The use of algae as the test organisms in such researches has continued in recent years with little abatement.

Another source of impetus to study of the physiology of algae is the prospect that mass culture techniques may be developed to a degree of practicality that will permit raising of algae as a supplementary source of food or raw materials. There is no doubt that such procedures are technically feasible; the major considera-tion yet to be resolved is whether or not they can also be made economically feasible. Substantial recognition of this possibility was made at the recent World

Symposium on Applied Solar Energy held in Tucson and Phoenix, Arizona, at which four full half day sessions were devoted to the green plant as a solar energy converter. By far the larger part of this time was devoted to the algae, and the possibility of mass culture of algae on a commercial basis received substantial consideration in the deliberations.

Fungus physiology is another branch of plant physiology which has received increasing emphasis over the past decade or two. Less than a generation ago only one botany department in this country offered a course in the physiology of the fungi; today practically every major botany department in the country lists such a course among its offerings. A major source of impetus to increased interest in fungus physiology has been the discovery that certain species of fungi are important sources of antibiotics. The discovery of penicillin and the subsequent development of its production on a commercial scale is a story which is well-known to every enlightened citizen.

Although fungi lack the fundamental solar energy conversion feature of metabolism which is the basic process of chlorophyllous plants, nevertheless their metabolisms are often so distinctive as to result in the synthesis of compounds which are useful to man. By proper selection of species and varieties, by development of the most suitable cultural conditions, and by the use of large scale industrial production techniques, certain so-called fermentation processes of fungi have been used for the commercial production of various useful compounds. The best known of these are ethyl alcohol and citric acid.

Latterly, wide use has been made in a practical way of the propensity of certain fungi to synthesize, as previously mentioned, certain complex compounds which act in an antibiotic capacity. Among the better known of these are streptomycin, terramycin, and aureomycin, all of which are synthesized by fungi of the actinomycetes group. Gibberellic acid, previously mentioned, is the latest addition to the biologically significant compounds being used by man which is a synthetic product of a fungus.

Passing on to a brief consideration of the vascular plants, two main trends seem to be at work in the kinds of plants used in physiological experimentation. Although by no means a new tendency, increasingly certain investigators and groups of investigators have specialized in the physiology of one plant, usually a species of economic importance. Thus, we see emerging substantial bodies of knowledge regarding the physiology of the corn plant, the physiology of the cotton plant, the physiology of the tobacco plant, and so forth. It is hoped that eventually investigations channelled along such lines will bear fruit in the form of mongraphs dealing with the physiology of such individual species. This is a desirable approach since the physiological requirements and behavior of no two kinds of plants are identical; indeed even different varieties of the same species often differ appreciably in their physiology. A thorough knowledge of the basic physiology of each economic species of plant is one of the primary requisites for enlightened cultural practices. We should know about the mineral nutrition, photoperiodic behavior, temperature relations, drought resistance, cold resistance, seed viability, dormancy of various organs, pollen viability, water requirement, light saturation for photosynthesis, and many other physiological characteristics of each such species. Much remains to be done along these lines.

Another increasing trend among workers with vascular plants has been that of intensive investigations of phsyiological phenomena in certain "guinea pig" species of plants. One advantage which the general plant physiologist enjoys as compared with the "one species" plant physiologist is that of choice in selection of his experimental plants. Some kinds of plants are intrinsically better adapted to certain kinds of physiological experimentation than others.

One well-known example of this trend is the extensive use of the oat coleoptile as the test object in biological assays of auxins. When oat coleoptiles are allowed

to develop for a limited time in the dark under certain conditions of temperature and humidity and especially if decapitated, the quantity of enodgenous auxin present becomes very low, making such coleoptiles extremely sensitive to auxins from an external source. Within limits the growth or curvature of such coleoptiles can be used as a quantitative index of the amount of auxin with which it is brought into contact. A further advantage of oat coleoptiles as test objects is that large quantities of them can be raised in a small space, permitting many replications of a given test to be made with relative ease.

A similar example is the extensive use of the cocklebur as a test plant in photoperiodism experiments. In fact this is the only known use of cockleburs to the human race! This common weed species is distinctive in that only one short day photoperiodic cycle is sufficient to induce initiation of flower primordia in plants which are otherwise kept under long day conditions. To the best of my knowledge there is only one other species of which this is known to be true. In ways which any specialist on photoperiodism will recognize, the extreme photoperiodic sensitivity of this species has made it an uncommonly useful test plant in many studies of this phenomenon.

More practical minded plant scientists sometimes comment in a dubious or even sarcastic vein on what seems to them, the often unrealistic or even bizarre selections of experimental plants made by physiologists working on basic problems in the field. There is a commonly quoted statement, which originated, I believe, in the medical field, to the effect that "normal physiology is often revealed only by pathological conditions." There is a sound element of truth in this statement, but I do not believe it is a broad enough generalization. Behavior as revealed by species which are genetically unusual often helps in understanding reactions of other species in which the existence of certain reactions is less marked. Likewise, insight into physiological reactions or behavior under usual or normal patterns of environmental conditions are often revealed by subjection of plants to unusual or abnormal conditions. Reactions which are not otherwise apparent are often brought to light in this manner.

Since this is a symposium on forest physiology, I would like to be able to add that there has been a strong trend toward increased work on forest trees by plant physiologists in recent years. I believe there is a trend in that direction but cannot honestly say that it seems to be a pronounced one. The average plant physiologist looks at a full-grown tree, shakes his head, and turns his research endeavors in other directions, to work with *Chlorella*, perhaps, or maybe with bean plants. A tree is not a good laboratory plant for the same reasons that an elephant is not a good laboratory animal.

Actually, of course, the foregoing remarks are not a wholly accurate appraisal of the situation. While it is seldom possible to subject large, mature trees to laboratory or greenhouse experimentation, wide horizons are open for physiological research with tree seeds, cuttings, seedlings and small trees. And work with large trees is not precluded either although for such investigations the laboratory must go to the tree, rather than the tree go to the laboratory.

There are indications that we are on the threshold of a revitalized interest in tree physiology. This symposium is one evidence of such an increase in interest. Similar symposia held at Petersham, Massachusetts just recently and at Ottawa, Canada about two years ago are further such evidence. And just this past year there has been published a "Tree Physiology Bibliography," compiled by Dr. Theodore T. Kozlowski of the University of Massachusetts in cooperation with the U. S. Forest Service. About 4000 titles are listed in this bibliography. I do not believe it is any secret that Dr. Kozlowski, in co-authorship with Dr. Paul J. Kramer of Duke University, now has in an advanced stage of preparation the manuscript for a book on tree physiology. This will be a welcome addition to the literature, since such books and monographs as have been published in this general field of knowledge are long outdated.

And, in conclusion, I wish to say a few words about not what is a trend, but perhaps should be one.   More than once I have heard this statement: "A botanist is a kind of a scientist who usually starts out with a living plant and most commonly ends up with a dead one."   This is an indictment which cannot be too easily shrugged off.   Consider the taxonomist who collects live plants and dries them into extinction; consider the morphologist who collects live plants and pickles them into extinction; consider the physiologist who collects live plants and grinds them into extinction.   Although the above statement is admittedly a somewhat exaggerated one, there is nevertheless a valid element of irony in it.   Botany is a life science, yet we work too much of the time with corpses, and sometimes un-recognizable corpses at that.   Some of this is unavoidable, but let's keep as much life in our plants as possible.   We need to put more emphasis on techniques which the plants can survive as living entities.   We have some such techniques, but perhaps not enough.   Perhaps one possibility would be a more extensive adoption of the biopsy techniques used by our colleagues in the medical sciences.

The great miracle of life is that it has evolved into and persisted in a thermo-dynamically inhospitable world.   We owe a respect, and perhaps even a reverence, for this achievement by even the least human of living organisms.   We should never forget that, as plant scientists, we are dealing with a basic and significant manifestation of life.   I quote from the incomparable Emily Dickinson, who with the poet's true intuition, saw the same matter in a slightly different, but pertinent, context:

> "Surgeons must be very careful
> When they take the knife!
> Underneath their fine incisions
> Stirs the culprit—Life!"

TRANSLOCATION IN TREES[1]

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In this discussion we shall use the term "translocation" to refer to the movement or transport of water and solutes over distances of considerable magnitude relative to the size of the plant.   In the larger trees, this distance may be enormous even in absolute terms, several hundreds of feet, and in the case of certain tropical lianas, closer to a thousand feet.

We are much indebted to forest physiologists for many significant advances in this study.   Because of the large size *per se* of trees, they provide excellent material for the investigation of many specific problems in translocation, and it is clearly evident from the literature that some of the most critical data we have on this subject have been obtained from such species.

Translocation may be conveniently considered under three subdivisions: the translocation (1) of water, (2) of mineral solutes, and (3) of organic solutes.   The broad scope of this subject and the limitations of time will permit only a very cursory survey of these areas of research.

WATER TRANSLOCATION

The problem of the ascent of water in trees is one of the oldest in plant phy-siology. Interest in this problem reached a climax just prior to the turn of the century with the publication in 1894 of the Dixon-Joly water cohesion-trans-pirational pull or liquid tension theory. With minor modifications, this theory has been universally accepted for presentation in standard text-books of botany and plant physiology, and the general outlines of this concept are, therefore, well known. This theory provided such a plausible mechanism for the translocation of water that the problem was considered quite satisfactorily solved, and interest in the actual process of water conduction diminished in subsequent years. In rather recent years, however, a number of papers highly critical of the cohesion theory have been published, and it appears now that interest in the problem is gradually being renewed. The present status of the problem has been reviewed recently by Greenidge (1957).

One of the major points of controversy is the tensile strength of water under the actual conditions which obtain during the flow of water through the tracheids and vessels of the xylem. Published values for the cohesive strength of water, arrived at by a variety of techniques and under a variety of conditions, range from only 0.05 atm. to the extremely high values of the order of 15,000 atm. It is commonly accepted that a minimal tensile strength of 20 to 30 atm is required to lift water to the tops of the tallest trees; a critical experiment, therefore, would be to demon-strate conclusively that the tensile strength of water in the conducting elements of the xylem is significantly less than this value.

One technique for determining the limiting negative pressure or tensile strength of water is to measure the force in a centrifugal field required to break a column of water held in a glass capillary. Under rigorously defined conditions, the limiting negative pressure as determined by this method is of the order of 200 atm. at room temperatures, but falls off rapidly at temperatures below 5°C to values of about 20 atm. near 0°C (Briggs, 1950). Thus, it would appear that during the winter season, the tensile strength of the sap is at or near the critical value which permits cavitation, even if the values obtained for water under ideal conditions are adopted. Recently, Scholander *et. al.* (1955) attempted to measure the limiting negative pressure of xylem sap in sections of grape vine stems, using a centrifugation tech-nique. Even though the water columns were under static conditions (non-moving), practically all vessels were found to cavitate under stresses as low as 1 to 1.5 atm. Although the limitations of the centrifugation technique as applied to stem sections must be assessed before these values can be critically accepted, the results of the experiments by Scholander *et. al.* presently indicate disturbingly low values.

Further observations critical of the cohesion mechanism have been provided by the *double saw-cut* technique, a procedure utilized most extensively by Greenidge (1955). Using forest grown trees, Greenidge interrupted all of the vessels in the trunks by making overlapping saw-cuts from opposite sides of the bole slightly more than half way through the tree, the vertical distance separating the cuts being less than the average length of the vessel member or segment of the species under consideration. Presumably, therefore, the liquid columns in all vessels were exposed to atmospheric pressure. Despite these drastic treatments, dye solutions injected into the tree trunks below the lower saw-cut moved rapidly into the terminal branches of the crown. It is difficult, of course, to reconcile these results with the classical concept of the Dixon-Joly mechanism. Although an indeterminate fraction of the water, in Greenidge's experiments, undoubtedly circumvented the incisions by lateral movement through the tracheids, evidence was also obtained, based on staining patterns, that mechanical interruption of the water columns did not lead to wholesale evacuation of the vessel contents, as re-quired by classical theory if the columns were under tension. Rather, the evidence

pointed to only a slight retraction of the menisci at the cut surfaces, a phenomenon which, if correctly inferred, is most difficult to explain. A more plausible interpretation, however, may be that the vessel walls were stained by absorption of dye from the water moving through tracheids contiguous to the vessels.

Various other disturbing observations have been reported, and it is not clear in all cases by what criteria they can be dismissed, unless it be, as has been remarked by others, that equally great or greater difficulties will then be encountered. Although the Dixon-Joly liquid-tension concept continues to be our best explanation, it is evident that one of the more quiescent problems in plant physiology has been considerably reactivated in recent years by continuing work and interest in tree physiology.

MINERAL SOLUTE TRANSLOCATION

An extensive literature is available on the subject of mineral solute translocation, based mainly on agronomic crop plants and other herbaceous type plants, but significant contributions to this area of research have also been made using arborescent species. The specific subject of mineral translocation in trees has been recently reviewed by Fraser (1956).

The relative roles of the xylem and phloem in the upward translocation of minerals has been much debated in the literature. The general consensus appears to be that the initial upward transport of the minerals from the roots to the leaves occurs predominantly in the xylem, with subsequent re-translocation in the phloem. This view has been arrived at mostly from studies on herbaceous plants. Recently, however, Fraser (1956), noting the intense localization of Ca^{45} in the sieve cells of white pine trees which had been injected with this isotope near the base of the trunk, has suggested that, in trees, the phloem tissue may be more important than the xylem in upward transport of mineral salts. It cannot be ruled out, however, from Fraser's studies that this distribution pattern did not result simply from lateral accumulation of calcium ions from the xylem. As a matter of fact, most studies reveal that calcium compounds are singularly immobile in the phloem (see review by Gauch, 1957). Fraser's view, however, conforms with that of MacDaniels and Curtis (1930). When apple trees were spirally ringed, it was noted that nitrogen from the roots moved principally to the branches above the open end of the spiral, whereas branches on the opposite side of the tree received relatively little nitrogen. Although the tracheary sap of apple trees contains moderate concentrations of nitrogenous compounds throughout the growing season (Bollard, 1953), it seems apparent that the amount of nitrogen compounds transported by way of the phloem from the roots in the experiments of MacDaniels and Curtis was sufficiently greater than that transported in the xylem to control the major distribution pattern of this element in the crown. It is evident that further work must be carried out on this problem before the relative efficiency of the phloem and xylem in upward mineral transport can be quantized with greater accuracy than is now possible. The weight of the evidence from most species studied still strongly favors the classical view of the xylem as the predominant pathway of transport, although a number of apparently contradictory observations remain to be reconciled on this basis.

As previously remarked, calcium is considered one of the phloem-immobile elements. Presumably for this reason, re-translocation of calcium in plants, after its initial movement from the roots to the leaves or other depots, is negligible, inasmuch as the export of minerals in general (perhaps mostly as metal-organic complexes) from the leaves is apparently phloem-limited for the most part. This view has been gained, however, from studies on annuals, and recently Ferrell and Johnson (1956) have reported results which indicate considerable calcium mobility in trees (western white pines). Buds which were produced one and even two years after the time of injection of Ca^{45} were found to have appreciable concentrations

of the labeled calcium (corrected for radioisotopic decay). It is possible that this indicated mobility is only apparent, resulting from a leaching of the calcium from the leaves by rain, and subsequent re-entry into the tree from the soil. It is known that calcium and other mineral ions are readily leached from leaves (Tamm, 1951; Long *et. al.*, 1956) but the decline each year in the specific activity of the calcium in the buds, in most trees studied, was relatively small, and this fact favors the view that the calcium was redistributed directly from deposition sites in the tissues of the previous year to the new tissues, but whether this re-translocation was effected mainly by way of the phloem or the xylem is not known.

ORGANIC SOLUTE TRANSLOCATION

The translocation of organic solutes from one part of a plant to another is a process of considerable magnitude, greater than that of mineral solute translocation, and second, in quantitative terms only to water translocation. An apple orchard, for example, will, under very favorable growing conditions, produce in excess of 60,000 pounds of fruit per acre, containing approximately 4 to 4.5 tons of organic substances. Only a small fraction of this organic increment is the result of photosynthesis in the fruit itself; the much greater fraction is derived from compounds translocated to it from the leaves. Although it may be objected that these large values derive from the acreage basis used in these calculations, the process may be of very sizeable magnitude even at the individual fruit level. In the Zucca melon, for example, a single fruit may attain a dry weight of five pounds. Assuming an average molar weight of 300 grams for the translocatory compounds (on the basis that the translocate is mostly sucrose), and disregarding various second order corrections, approximately 4.5×10^{24} molecules of the organic translocate would have to move into such a fruit to account for the dry weight increase. This number of molecules, if sucrose, placed end to end, would extend a distance of 2.5 trillion miles. It should not be construed, of course, that the molecules are translocated single file; the computation merely serves to emphasize the enormity of the number.

An elegant approach to the problem of organic translocation in trees has been the chromatographic analysis of the sieve tube exudate. A considerable number of such studies have now been made by various investigators (Kennedy and Mittler, 1953; Wanner, 1953; Ziegler, 1956; Zimmermann, 1957a, b, c). The technique is limited, of course, to such species which yield an exudate when the sieve tubes are tapped, but it is possible that utilization of Kennedy and Mittler's aphid technique (1953) may considerably extend the number of species which can be studied. The results of these studies may be briefly summarized as follows. Sucrose was found to be present in the sieve tube exudate of all species thus far studied (about 25), and was the only sugar present in about a third of these species. In the remaining species, raffinose was also found, and in a few species, stachyose and perhaps verbascose, as well. These sugars form a series of oligosaccharides differing from each other in the number of included galactose residues (sucrose none, raffinose one, stachyose two, etc.). During transit within the sieve tubes, these sugars may undergo at least a limited amount of interconversion, for example, stachyose to raffinose to sucrose, although no positive test has yet been obtained for galactose, which would also be produced in these reactions (Zimmermann, 1957a). It is also noteworthy that neither glucose nor fructose has been found in any of the sieve tube exudates thus far tested. These data suggest that hexose sugars do not function in translocation.

A similar conclusion with respect to the translocation of sugars in the Concord grape was reached by Swanson (1957) and Swanson and El Shishiny (1957) based on radiochemical studies using C 14. The carbon label was introduced by supplying $C^{14}O_2$ to a single leaf on the cane under conditions favorable for photosynthesis. In sugar fractions isolated from the stem (bark) at various distances from

the supply leaf, the highest percentage recovery of C–14 was found to be in sucrose. Appreciable quantities of C–14 labeled glucose and fructose were also found in the bark, but these sugars appeared to be simply hydrolytic products of translocatory sucrose, as inferred from the fact that the ratio of C–14 glucose to C–14 fructose approximated unity.   Evidently sucrose molecules which escape from the sieve tubes are readily hydrolyzed to invert sugars in other cells of the phloem and adjacent tissues.   The present indications are, therefore, that sucrose is a specific sugar of transport, at least in certain species.

The amino acid content of sieve tube exudates has not been as critically studied as has the carbohydrate content, primarily because of the negligible quanity of this fraction in the exudate.   In the sieve tube exudate of white ash, for example, the total amino acid content was usually less than 0.001 M, as contrasted with 0.3 to 0.4 M and higher for the total sugars (Zimmermann, 1957b, c).   It thus appears that the types of compounds which are transported over relatively great distances in the phloem in *calorically significant* quantities are quite few in number, being predominantly sugars of the raffinose family, and perhaps in some species, specifically and exclusively sucrose.   In this connection it should be noted that fruit culture studies have shown that excised tomato and gherkin ovularies (ovaries) can grow *in vitro* and form fruits which may occasionally even produce viable seeds on a culture medium containing only sucrose, mineral salts, and water (Leopold *et. al.*, 1952; Nitsch, 1951).   Recently Erickson (1957) reported that grafting immature sour lemon fruits, without scion leaves, on a sweet lemon tree, and vice versa, did not materially change the organic acid composition of the respective fruits when mature.   Evidently the organic composition of such fruits, perhaps of fruits in general, is quite independent of the composition of the phloem translocate reaching the fruits from the leaves, or alternatively, the composition of this translocate is essentially the same in many different species (predominately sucrose and related sugars) and biochemical differentiation occurs almost entirely *in situ*, in the same manner as different tissues may be cultured on the same simple substrate.   It is not known at present what fraction of the nitrogen and other mineral constituents of the fruit are derived from materials entering via the phloem and what fraction from those entering via the xylem.   The organic acid content (mainly amino acids) of the tracheary sap of many species of trees (Bollard, 1956) is considerably higher than that of sieve tubes.   It is conceivable, therefore, that nitrogen, and other mineral elements as well, are supplied to the fruit principally through the xylem.

The mechanism of organic translocation has engaged the attention of numerous plant physiologists.   We shall not enter here into a discussion of this highly controversial subject, but suffice it to state that the well-known pressure-flow hypothesis, formulated by the forest physiologist Münch (1930) continues to be a highly provocative and productive concept.   Recently, Zimmermann (1957c), another forest physiologist, has made an interesting application of this hypothesis to explain gradient reversals in the sieve tubes of white ash.   There is no question about the impact of Münch's hypothesis on the thinking of plant physiologists. It is on this note that I wish to conclude this very cursory review of translocation, a note of recognition of our indebtedness to forest physiologists for their many significant contributions to fundamental problems in general plant physiology.

<div align="center">LITERATURE CITED</div>

Bollard, E. G.   1953.   The use of tracheal sap in the study of apple-tree nutrition.   Jour. Exp. Bot. 4: 363–368.
————.   1956.   Nitrogenous compounds in plant xylem sap.   Nature 178: 1189–1190.
Briggs, L. J.   1950.   Limiting negative pressure of water.   Jour. Appl. Physics 21: 721–722.
Erickson, L. C.   1957.   Citrus fruit grafting.   Science 125: 994.
Ferrel, W. K. and F. D. Johnson.   1956.   Mobility of calcium–45 after injection into western white pine.   Science 124: 364–365.

Fraser, D. A.   1956.   The translocation of minerals in trees.   Dept. Northern Affairs and
    National Resources.   Forest Research Division.   Canada.   Tech. Note No. 47.   pp. 1 16.
Gauch, H. G.   1957.   Mineral nutrition of plants.   Ann. Rev. Plant Physiol.   8: 31–64.
Greenidge, K. N. H.   1955.   Studies in the physiology of forest trees.   III.   The effect of drastic
    interruption of conducting tissues on moisture movement.   Amer. Jour. Bot.   42: 582–587.
————.   1957.   Ascent of sap.   Ann. Rev. Plant Physiol.   8: 237–256.
Kennedy, J. S. and T. E. Mittler.   1953.   A method of obtaining phloem sap via the mouth-
    parts of aphids.   Nature 171: 528–529.
Leopold, A. C. and F. J. Scott.   1952.   Physiological factors in tomato fruit-set.   Amer. Jour.
    Bot. 39: 310–317.
Long, W. G., D. V. Sweet, and H. B. Tukey.   1956.   Loss of nutrients from plant foliage by
    leaching as indicated by radioisotopes.   Science 123: 1039–1040.
MacDaniels, L. H. and O. F. Curtis.   1930.   The effect of spiral ringing on solute translocation
    and the structure of the regenerated tissues of the apple.   Cornell Univ. Agr. Exp. Sta.
    Mem No. 133.
Münch, E.   1930.   Die Stoffbewegungen in der Pflanze.   Gustav Fischer.   Jena.
Nitsch, J. P.   1951.   Growth and development in vitro of excised ovaries.   Amer. Jour. Bot.
    38: 566–577.
Scholander, P. F., W. E. Love, and J. W. Kanwisher.   1955.   The rise of sap in tall grapevines.
    Plant Physiol.   30: 93–104.
Swanson, C. A.   Translocation of organic solutes.   1957.   In "Atomic Energy and Agriculture."
    Amer. Assoc. Advancement Sci., Washington, D.C.
—— —and E. D. H. El Shishiny.   Translocation of sugars in grape.   Plant Physiol.   (In press).
Tamm, C. O.   1951.   Removal of plant nutrients from tree crowns by rain.   Physiol. Plant.
    4: 184–188.
Wanner, H.   1953.   Die Zusammensetzung des Siebröhensaftes: Kohlenhydrat.   Ber. schweiz.
    botan. Ges. 63: 162–168.
Ziegler, H.   1956.   Untersuchungen über die Leitung und Sekretion der Assimilate.   Planta
    47: 447–500.
Zimmermann, M. H.   1957a.   Translocation of organic substances in trees.   I.   The nature of
    the sugars in the sieve tube exudate of trees.   Plant Physiol.   32: 288–291.
————.   1957b.   Translocation of organic substances in trees.   II.   On the translocation
    mechanism in the phloem of white ash.   Plant Physiol.   32 (in press).
————.   1957c.   Translocation of organic substances in the phloem of trees.   Paper presented
    at the Cabot Foundation Symposium on Tree Physiology, Petersham, Mass.

DISCUSSION

DENNIS RICHARDSON (*University of Aberdeen, Scotland*): In view of the recent evidence of rapid sugar transformation in plants, do you think that observed temperature coefficients for carbohydrate translocation can be interpreted as illustrating *direct* effects of temperature in sucrose transport?

C. A. SWANSON: So far as I know, the experiments required to give a good answer to this question have not been carried out as yet. The pertinent data which have been published rest on indirect criteria for assessing the effect of temperature on carbohydrate transport and provide little information, therefore, on the specific effects of temperature on sucrose transport *per se*, or even on the effects of sugar interconversions and transformations on translocation rates. I believe it would be of interest to study certain of these effects by varying the temperature of a restricted zone of the stem, and subsequently analyzing the comparative distribution of the C–14 label in compounds from regions of the stem, or preferably the phloem, both proximal and distal to the temperature zone. Mr. Burley of our department has, as a matter of fact, given some consideration to such a problem, but no actual work is as yet underway.

DENNIS RICHARDSON: If Went's experiments indicating a Q_{10} for translocation of less than unity are explained on the grounds that he was measuring temperature effects on sugar transformation, not translocation, does not this argument apply equally to work which implies a Q_{10} greater-than unity?

C. A. SWANSON: With present information, I believe the only fair answer to this question is "Yes."

THE MINERAL NUTRIENT REQUIREMENTS OF FOREST TREES

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Substantial increases in tree growth following the application of mineral fertilizers have been reported from a number of countries, and it is now generally recognized that many soils under forest cover or available for reforestation are deficient in mineral nutrients. Whether fertilizing on the scale appropriate to the management of large areas is economically worthwhile is still somewhat controversial, but there is little doubt that with increasing awareness of the advantages to be gained from a more intensive silvicultural program, the potential benefits of fertilizing are receiving serious attention. The immediate problem is to decide whether the establishment or growth of a tree crop on a particular site is indeed limited by nutrient deficiencies and if so, what and how much fertilizer to apply. At the same time, because of the present lack of data, some knowledge of the total mineral nutrient demand of the forest stand on the soil is also desirable in view of the not inconsiderable amounts of nutrients removed from the site in logging.

As far as deficiencies are concerned, actual fertilizer trials in the field will of course most readily provide the answer but such trials are costly and time consuming; furthermore, they suffer from the disadvantage that the results are generally limited to the site and species under investigation at the particular time. Nor has soil analysis provided more than a general guide to the problem of tree nutrient requirements. As a result of the differentiation of distinct horizons, often differing appreciably in composition and rooting capacity, most forest soils are markedly heterogenous; this, together with the long periods of growth concerned and the well known limitations of conventional extraction procedures, severely limits the value of this approach.

An alternative approach is provided by studying the actual mineral composition of the tissues of the trees themselves, in particular the composition of the foliage since this is usually considered as providing the most sensitive indicator of the sufficiency or otherwise of the nutrient supply to the trees. This foliar diagnostic approach has been widely applied to agricultural and horticultural crops and earlier investigations, especially those of Mitchell (1939) and Mitchell and Chandler (1939), have confirmed its potential value in the study on the mineral nutrient requirements of forest trees. However, for a consistent and successful application of this technique, an understanding of the relationship between tree growth and the mineral composition of the foliage, both in relation to supply and other factors affecting this relationship, is essential. Failure to appreciate this and the limitations imposed on diagnostic interpretations has, in many cases, led to false conclusions and often invalid criticism.

As it is most simply and commonly interpreted, foliar diagnosis is based on the assumption that a deficiency in a particular nutrient is reflected in a subnormal content of that nutrient in the foliage or in an abnormal balance with respect to other nutrients or in both of these. This assumption implies the existence of a *normal or minimum* foliar content, and in the choice of standards of comparison a popular approach has been to select well grown specimens of the species and age concerned. However, it is well known that even in the same tree the composition of the foliage is not constant but varies according to its location on the crown, its age (*i.e.*, in conifers bearing more than one year's needles), and the time

of the year. Hence, in applying the concept of normal composition it is essential that the sample of foliage be so defined as to allow for a valid comparison between individuals. It is now more or less generally accepted that the most suitable time for sampling is when the variation in leaf composition with time is at a minimum, thus, just before yellowing in deciduous trees and sometime after the end of the growing season in conifers. Somewhat less attention has been paid to the location and age of the foliage although this would appear to be of considerable importance. Presumably the most suitable sample should reflect to the greatest degree differences between trees of varying nutritional status and vigor. According to recent investigations of Leyton and Armson (1956) on Scots pine of varying heights in an even aged plantation, this condition is provided only by current needles from the terminal or uppermost lateral shoots; in this particular case, older needles or those taken from lower down the crown revealed little consistent change in composition with tree vigor and it is possible that many of the reported failures to relate growth to foliar composition can be attributed to incorrect sampling.

A major objection to the use of healthy well grown trees as standards of comparison is that the foliage of a selection of such trees, even when sampled under identical conditions, may differ appreciably in composition because of the phenomenon of *luxury consumption*, *i.e.*, nutrient uptake in excess of actual growth requirements without any apparent influence on growth. Under these circumstances simple comparisons between individuals may lead to errors in diagnosis.

More reliable data on optimum nutritional conditions have been obtained experimentally by growing trees in cultures with an adequate supply of all nutrients other than the one in question and by following the response in growth and in foliar composition to increasing supplies of that nutrient. In this way Mitchell (1939) demonstrated, for white pine seedlings, a curvilinear relation (diminishing returns) between supply and growth and between growth and the concentration of the limiting nutrient in the foliage dry weight. Similar relations have been established for older specimens of a number of tree species in the field, *e.g.* by Mitchell and Chandler (1939) for various hardwoods, by Tamm (1956) for Scots pine, and by the author for Sitka spruce and Corsican pine (fig. 1 and 2). Generally there is evidence for the occurrence of maximum growth (under the prescribed experimental conditions) at a particular optimum concentration characteristic of the nutrient and species concerned, *e.g.*, in the above cases of spruce and pine at optimum P concentrations of 0.13 and 0.15 percent, respectively. At higher concentrations there is a tendency for growth to fall, though this is probably due to the influence of high levels of supply on the uptake of other nutrients rather than to a so-called toxic effect of high concentrations in the foliage per se.

A qualification to the relationships established above is suggested by observations of an initial fall in concentration with increasing supply and growth giving a sigmoid shaped curve (Steenbjerg, 1954). In the case of micro-nutrients for example, this may be brought about by a disproportionately large response in growth to a small increase in supply. Though similar phenomena have been occasionally claimed for the major elements, no evidence of these has yet been put forward for forest tree species, especially under field conditions.

From the nature of the curve relating growth to foliar composition, it is evident that over a large part of the deficiency range and *only within this range*, growth and concentration of a limiting nutrient are linearly and positively related, or at least the regression of one on the other yields only a significant linear component. If the converse were equally valid, it would mean that the establishment of a positive linear correlation between growth and the concentration of a particular nutrient in the foliage would signify a deficiency in that nutrient. Such correlations have indeed been found on a number of occasions where proof of a deficiency has subsequently been established. For example, in the case of Sitka spruce growing on a
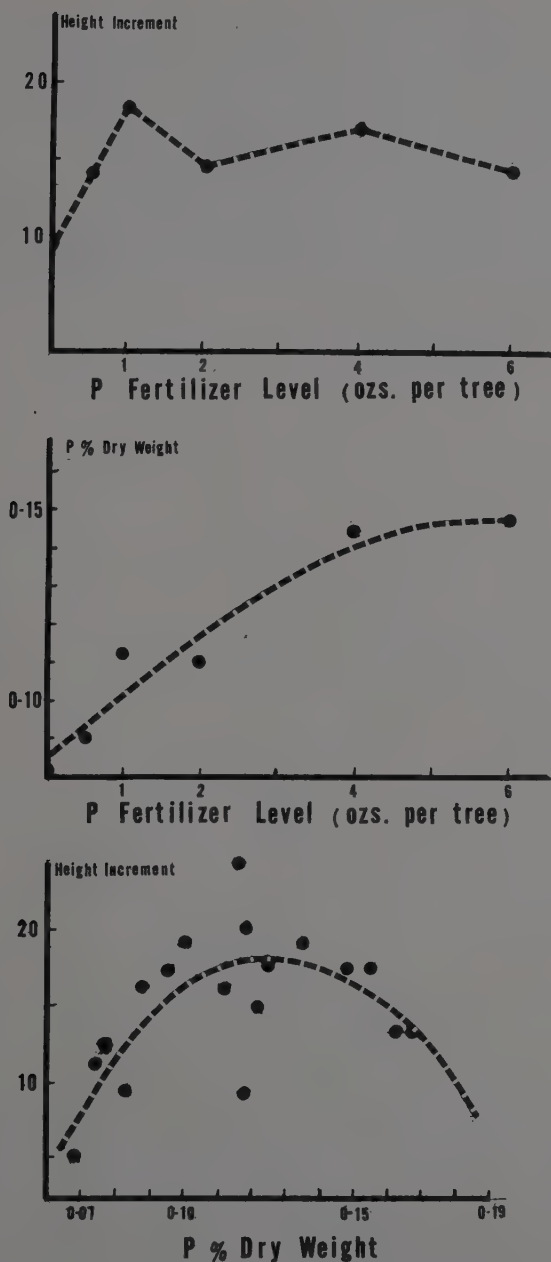
FIGURE 1. Sitka spruce. Relationship between phosphate supply, height increment, and P content of current needles (% D. Wt.).

heathland site in Britain, significant linear relationship between tree height or mean needle weight and the nitrogen concentration in the foliage were confirmed as reflecting a nitrogen deficiency by subsequent responses in growth to nitrogenous fertilizers (fig. 3; also Leyton, 1954). On the other hand, because of mutual interrelations between nutrients, false correlations of this kind are also possible. A particularly interesting example of these was provided by an investigation into the nutritional relationships of young even-aged Japanese larch trees growing on a heterogenous site and showing considerable variation in height growth. In this case (Leyton, 1956) significant linear relations were established between tree height and the concentrations of the nutrients N, P, K, and Ca in the foliage. However, from the analysis of the multiple regression of height on these
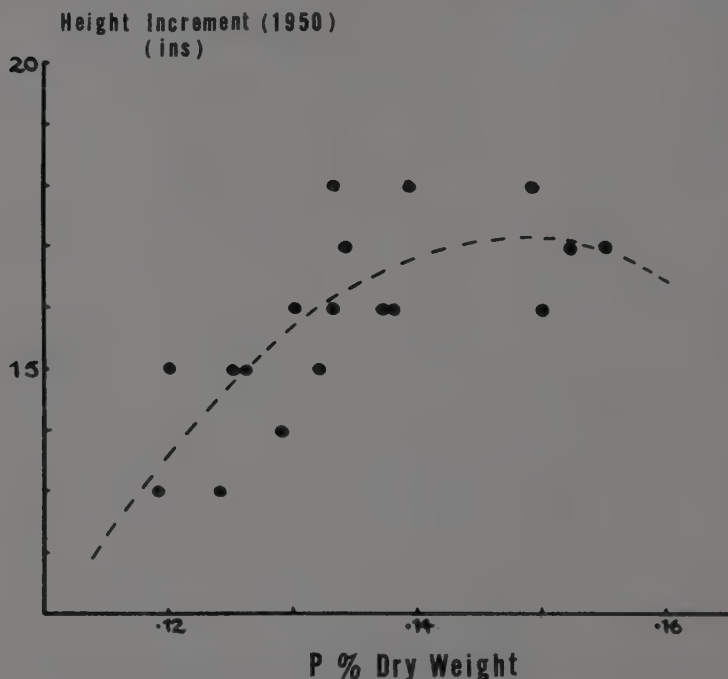
FIGURE 2. Corsican pine. Relationship between height increment and P content of current needles (% D. Wt.).

nutrient factors, it was found that only N, and to a lesser extent K, made significant contributions to the regression and that the apparent relation of growth to P and Ca arose out of significant internal relations between these and the significant nutrient factors. Subsequent fertilizer trials revealed the existence of marked N deficiencies and lesser K deficiencies in these trees, thus confirming the deductions based on analysis of the nutritional relationships (Leyton, 1957).

The important problem remains as to how far relationships between tree growth and foliar composition, of the kind discussed above, are affected by other factors such as environment and tree age. Are the optimum concentrations found

in the above examples peculiar to the particular experimental conditions under which they were determined or are they of wider application? In those cases where the availability of a particular nutrient is the sole factor determining growth, the relationship between supply, growth, and concentration is uniquely determined; under natural conditions such a situation is largely hypothetical since, in the field at least, growth is invariably influenced to a greater or lesser extent by many factors other than the availability of a single nutrient. In many cases, especially on very infertile soils, responses in tree growth may be obtained to increased sup-
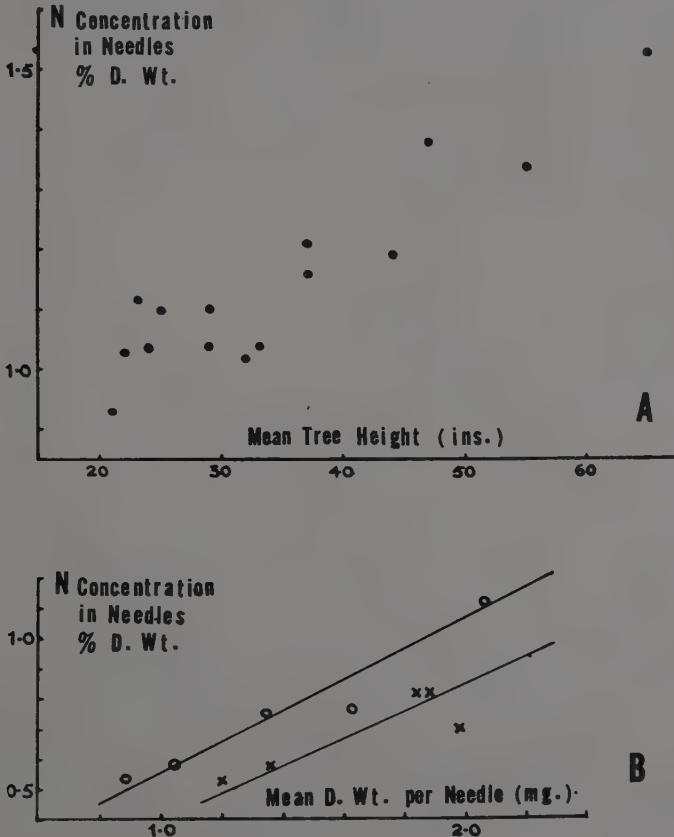
FIGURE 3. Sitka spruce on heathland. A. Relationship between mean tree height and N content of current needles (% D. Wt.). B. Relationship between mean needle dry weight and N content. x—x, control plots. 0—0, treated with P fertilizer.

plies of different nutrients revealing the existence of multiple deficiencies. An example of this was provided by the case of the Japanese larch mentioned above and the relationships involved could be analyzed by multiple regressions. This approach suggested that in terms of their concentration in the needle dry weight, each nutrient could be considered independently as making their separate contri-

butions to growth and furthermore that there was for each nutrient an optimum concentration independent of the influence of other factors (Leyton, 1957). These findings support earlier conclusions of Mitchell and Chandler (1939) that although the actual amount of growth at a particular concentration of a limiting nutrient in the foliage varied with site, maximum growth on different sites corresponded to more or less the same optimum concentration. Further support for this argument is provided by various other investigations. In the case of Japanese larch an optimum N concentration in the needles of about 2.8 percent dry weight has been established independent of fertilizer influences (Leyton, 1957) whilst the results of an independent investigation on seedlings of this species provided with different amounts of N and P (van Goor, 1953) suggest that maximum growth occurs at much the same value. This investigation also reveals an optimum P concentration of about 0.4 percent and it hardly seems coincidental that in a recent countrywide survey of the P status of young transplants of this species, in relation to their growth and response to P fertilizers (fig. 4), a similar optimum
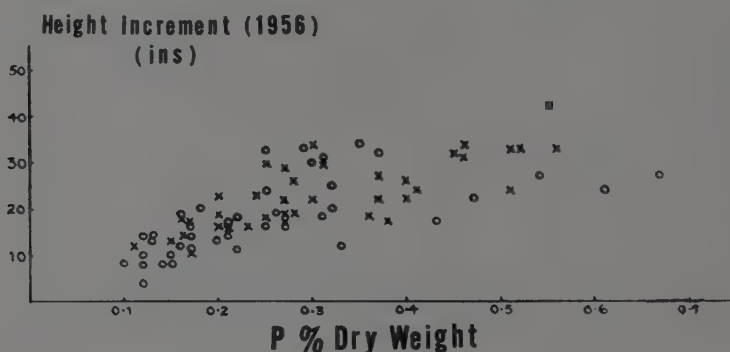

FIGURE 4. Japanese larch. P50 phosphate trials. Relationship between current height increment and P content of needles (% D. Wt.). 0—0, controls. x—x, treated with P fertilizer.

value is suggested. It is perhaps of no less significance that in recent trials on older trees with P concentrations of this order, no response has been obtained to the application of P fertilizers (Leyton, 1957). Similarly, in an investigation on Sitka spruce (fig. 5), evidence is suggested for an optimum N concentration of about 1.6 percent whilst in other trials on this species with values below this, essentially linear relations between growth and N concentrations have been established (fig. 3).

On the evidence available, therefore, there would appear to be some justification for assuming that the concept of optimum nutrient concentrations for a particular species holds over a range of environmental conditions and age, though of course the actual amount of growth made will tend to vary according to other factors influencing growth. At the same time it will be appreciated that from a practical point of view the forester is concerned not so much with optimum levels (about which growth varies little with changes in nutrient supply) as with lower levels which correspond to definite deficiency conditions. Much attention has therefore been paid to the possible establishment of minimum or critical concentrations below which a response to the appropriate fertilizer can be expected with reasonable certainty. For adult trees in the field such information has been obtained from fertilizer trials in which growth responses can be related to the

concentration of a particular nutrient in the foliage. It must be emphasized, however, that in view of the nature of the response curve, there is probably no precise critical concentration but a range of concentrations below which growth increases rapidly with increasing supply and concentration and above which there is little change. From the data available in the literature to date, critical and optimum concentrations for a number of tree species have been summarized in table 1 below.

TABLE 1

Deficiency and optimum levels of foliage N, P, and K concentrations (% dry weight)

Species		Deficiency N	Deficiency P	Deficiency K	Optimum N	Optimum P	Optimum K	Authority
Pinus sylvestris	(S)				3.0			Gast (1937)
Pinus sylvestris	(F)	1.2 –1.3	.08					Tamm (1954)
Pinus strobus	(S)	.70–1.33	.10–.28	.82–1.02	3.26	.67	1.72	Mitchell (1939)
Pinus strobus	(F)			.34				Heiberg & White (1951)
Pinus resinosa	(F)			.34				Heiberg & White (1951)
Pinus corsicana	(F)					.15		Leyton (1954)
Picea abies	(F)	.80–1.0	.06					Tamm (1954)
Picea abies	(F)			.13–.21				Heiberg & White (1951)
Picea glauca	(F)			.13–.21				Heiberg & White (1951)
Picea sitchensis	(F)				1.5–1.6	.14		Leyton (1954)
Larix leptolepis	(F)				2.8	.40		Leyton (1957)
Betula spp	(F)	1.8 –2.1	.08–.10					Tamm (1954)
Populus tremuloides	(F)	2.0			2.6–2.8			Mitchell & Chandler (1939)
Acer saccharum	(F)	1.75			2.8–2.9			Mitchell & Chandler (1939)
Fraxinus americana	(F)	2.01			2.8–2.9			Mitchell & Chandler (1939)
Tilia americana	(F)	2.32			3.1–3.2			Mitchell & Chandler (1939)

(S) Seedling.   (F) Established trees in field.

In view of the still limited experimental proof of the constancy of the above values under all conditions, however, an unreserved acceptance of these limits is unwarranted.

In an alternative approach to the problem of foliar diagnosis, a number of investigations have stressed the importance for growth of a correct balance between nutrients in the foliage and especially in the case of the ratios N/P, N/K, and K/P, have proposed optimum values, a departure from which has been considered responsible for depressed growth. Investigations into the nutritional relations of Japanese larch (Leyton, 1957) have indeed disclosed an association of maximum growth with certain optimum values for such ratios and somewhat similar relationships have been established for Sitka spruce. There is also some evidence that these optimum values are of more general application insofar as N/P values calculated for Japanese larch in different parts of Britain correspond with each other and with values quoted by van Goor (1953) for seedlings of this species, namely 12.6, 14.7, and 9–12 respectively. When these values are compared with other estimated N/P optima, ranging from 12 to 15 for Scots pine (Boszormenyi, 1956), rubber (Beaufils, 1956) and oil palm (Prevot and Ollagnier, 1954), some

speculation as to a possible underlying common relationship in plant nutrition is unavoidable, especially when the various estimated optima for the N/K and K/P ratios also show some agreement. On the other hand, a careful inspection of the origin of these ratios would suggest that, rather than possessing some individual physiological significance, they merely offer an alternative reflection of relationships based on concentrations (Leyton, 1957).

Physiologically, there can be little doubt that neither the concentration nor the balance of nutrients in the foliage provide more than a reflection of the complex interaction between various nutrients and the metabolic responses resulting in growth. The fact that in most cases we are dealing with foliage at the end of the growing season when back translocation of mobile N, P, and K would presum-
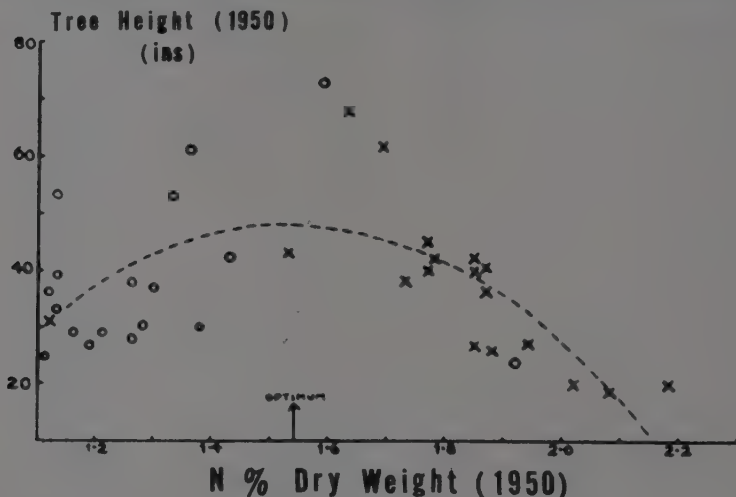
FIGURE 5. Sitka spruce on heathland. Relationship between tree height and N content of current needles (% D. Wt.). 0—0, controls. x—x, with surrounding heath vegetation removed by scalping.

ably have taken place, serves to emphasize the empirical nature of this approach in the study of tree nutrition. Nevertheless, if the physiological significance of these relationships is at present beyond our knowledge, their apparent consistency provides at least a valuable working basis for the determination of the nutrient requirements of trees. From a diagnostic point of view a stage has now been reached where foliar analysis, carried out with proper regard to sampling, would provide a reasonably consistent guide, not only to the nature and extent of a particular deficiency limiting growth, but also to the interpretation of many field observations. Because of the influence of other environmental factors like temperature and moisture on growth, data on foliar composition generally provide little information as to the extent of a growth response to a given increase in nutrient supply; of necessity this must be a limitation of all approaches other than actual field trials at the time in question.

REFERENCES

Beaufils, E. R.   1956.   Les equilibres minéraux dans les feuillage et dans le latex de l'Hevea Brasiliensis.   Ann. Agron. Paris 7: 203.

Boszormenyi, Z. 1956. Mineral nutrition of Scots pine seedlings I. Agrokemia es talajtan. Budapest, 5: 75.

Gast, P. R. 1937. Studies on the development of conifers in raw humus III. The growth of Scots pine seedlings in pot cultures. Med. Skogsforsoksanst. Stockh. **29**: 587.

van Goor, C. P. 1953. The influence of nitrogen on the growth of Japanese larch. Plant and Soil 5: 29.

Heiberg, S. D. and **D. P. White.** 1951. Potassium deficiency of reforested pine and spruce stands in northern New York. Proc. Soil Sci. Soc. Amer. 15: 369.

Leyton, L. 1954. The growth and mineral nutrition of spruce and pine in heathland plantations. Inst. Pap. Imp. For. Inst., Oxford, No. 31.

————. 1956. The relationship between the growth and mineral composition of the foliage of Japanese larch. Plant and Soil 7: 167.

————. 1957. The relationship between the growth and mineral composition of the foliage of Japanese larch. II. Evidence from manurial trials. Plant and Soil 9: 31.

Leyton, L. and **K. A. Armson.** 1956. Mineral composition of the foliage in relation to the growth of Scots pine. For. Sci. 1: 210.

Mitchell, H. L. 1939. The growth and nutrition of white pine seedlings in cultures into varying N, P, K, and Ca. Black Rock For. Bull. No. 9.

Mitchell, H. L. and **R. F. Chandler.** 1939. The nitrogen nutrition and growth of certain deciduous trees of northeastern United States. Black Rock For. Bull. No. 11.

Prevot, P. and **M. Ollagnier.** 1956. Peanut and oil palm foliar diagnosis. Interrelations of N, P, K, Ca, Mg. Plant Physiol. **29**: 26.

Steenbjerg, F. 1954. Manuring, plant production, and the chemical composition of the plant. Plant and Soil 5: 226.

Tamm, C. O. 1954. A study of forest nutrition by means of foliar analysis. Extrait de l'Analyse des plantes et problème des Engrais minéraux. 8th Congress Int. de Botanique. Ed. I.R.H.O., Paris.

————. 1956. Studies on forest nutrition III. The effect of supply of plant nutrients to a forest stand on a poor site. Med. Skogsforsoksanst. Stokh. 46(3).

SPECTROGRAPHIC TECHNIQUES AND ANALYSES OF PINE NEEDLES

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The spectrograph can be used to determine many elements in plants, although all elements cannot be determined equally well because of volatility, excitation, or ionization differences. Some 12 to 20 elements are rather easily determined in the open arc in plant ash in the procedure used here. They are boron, phosphorus, magnesium, lead, tin, silicon, iron, aluminum, molybdenum, calcium, vanadium, copper, silver, zinc, sodium, titanium, nickel, cobalt, wolfram, manganese, potassium, and chromium. Successful analyses can be made on very small samples on a spectrograph. Most samples are 100 milligrams in weight but smaller ones, down to 10 milligrams, can be used if necessary. This small sample size is an advantage when studying the margins and tips of leaves, especially the tips of pine needles.

In brief the spectrographic procedure consists of burning the samples in an open arc and recording the spectrum from this arc which contains the unknowns on a photographic plate. The spectrograms when properly developed and fixed constitute a permanent record of the elements in the samples. The light or radiation from the arc is dispersed through a quartz prism and each element shows up on the plate as a line of specific wave length or a group of lines characteristic of the element. The photographic emulsion also integrates the light energy from the elements and

forms a dense line when a quantity of the elements is present and a very faint line when only a small amount is present. This is the basis of the quantitative nature of the procedure.

The spectra of the elements on the plates are fine lines and must be examined and measured under a magnification of about 10 to 20 diameters for best results. Hence, a microdensitometer is a necessary part of the spectrographic laboratory.

METHODS

Location of lines.—The recognition, location, and determination of the origin of spectral lines could be a long job. But it is possible to locate and recognize those lines of the elements used in quantitative analysis in a few days time. The following is a list of those lines most commonly used to determine the given elements.

Element	*Angstrom*	*Element*	*Angstrom*
Boron	2497.7	Copper	3274.0
Phosphorus	2535.7	Silver	3280.0
Magnesium	2779.9	Zinc	3282.3
Lead	2833.1	Sodium	3302.3
Tin	2840.0	Titanium	3349.0
Silicon	2881.6	Nickel	3414.8
Iron	3020.6	Cobalt	3453.5
Aluminum	3092.7	Wolfram	4008.8
Molybdenum	3170.3	Manganese	4030.8
Calcium	3179.3	Potassium	4044.1
Vanadium	3184.0	Chromium	4254.3

The spectral lines are located (1) by means of an angstrom scale on the spectrograph, (2) by means of a reference spectrum, usually iron on high dispersion instruments or mercury on quartz prism spectrographs, or (3) by the characteristic pattern of lines for each element. Unconsciously all three methods may be used even though the angstrom scale or a reference spectra may not be consulted, or the pattern found. For with very little practice, the cyanogen bands or other known lines or groups of lines serve as a reference point and in a short time a dozen elements can be quickly recognized and measured.

Spectrographic arc.—The theory and construction of spectrographic sources is an involved and complicated study, but the practical use of such an arc is as simple as turning on and off an electric light. Flat top purified graphite electrodes are used to support the samples, and the arc or spark is maintained between them in the proper position in front of the spectrograph.

Plate calibration.—The photographic emulsion is not an ideal integrator of light energy. It may vary with the wavelength of light and not show a true linear response with intensity. It must be calibrated to show the amount of light necessary to produce a given blackening of the emulsion. This is an involved process and requires step sector discs, constant light source, special graph paper (Seidel paper), and controlled development of the plate. The end result is a table showing the transmission of the spectral lines and the intensity of light necessary to produce them. So all one has to do is read a table.

Working curves.—Working curves are constructed by plotting intensities from known amounts of the elements being studied. They are similar to working curves of substances determined in colorimetric analysis. They are made from synthetic mixtures of salts similar in composition to plant ash, with added known amounts of the required elements to be studied. Some are very easy to construct, but others, where enhancement or suppression of lines results from the presence of certain other elements or ions in the mixture, are very difficult to obtain.

TABLE 1

Boron content of red pine needle samples, from E. L. Stone, Professor Forest Soils, Cornell University. Plot B–12, 22 year old, sampled October 22, 1953 from mid node position, height 22 feet

| Sample Data | | | | | Spectrographic | | | | | Boron | |
Sample No.	Year growth	Needle tips cm	Dry. wt. gm	Per cent ash	Boron 2798 T	G	Lithium 2741 T	G	Ratio B/Li	μg in 10 mg ash	μg in 100 mg tissue
117	1953	0–1	.8	2.23	17	188	12.5	258	.73	29	6.5
					24	129	13	248	.52	18	4.0
118	1953	1–2	.7	1.52	30	100	10	327	.31	10.4	1.58
					28	108	9.2	356	.30	10	1.52
119	1953	2–	10.4	1.66	39	72.2	9	365	.20	6.5	1.08
					40	70.0	9.4	348	.20	6.5	1.08
120	1952	0–1	.9	3.02	12	269	9.8	333	.81	34	10.3
					16	200	10	327	.61	22	6.7
121	1952	1–2	1.0	2.03	41	67.9	10	327	.21	6.7	1.36
					35	83.0	8.5	393	.21	6.7	1.36
122	1952	2–	13.9	1.92	56	42.0	10	327	.13	3.4	.65
					53	45.8	9	365	.13	3.4	.65

No. = Original sample number, from E. L. Stone.
Cm = Part of needle in each sample, from tip down.
T   = Transmission in percent.
G.   = Gamma value or relative intensity.
Spectrographic Plate No. 26, Book No. 11, by David Chou.

TABLE 2

Elements in red pine needle samples

* No.	P 2536 G	Mg 2802 G	Pb 2833 G	Si 2882 G	Fe 3020 G	Al 3092 G	Ca 3179 G	Cu 3274 G	Ag 3280 G	Mn 4035 G	K 4044 G	Zn 4810 G	Li 2741 G
117	53	158	62	269	142	129	77	177	41	100	15	25	258
	47	136	66	248	136	123	66	167	43	86	14	26	248
118	46	149	62	80	50	77	86	230	49	72	24	19	327
	50	149	68	83	50	80	93	230	52	68	24	18	356
119	48	142	55	70	230	60	66	89	49	64	29	15	365
	42	136	62	66	113	53	66	96	53	53	25	14	348
120	53	89	43	258	129	136	108	136	33	177	9	14	333
	37	83	68	230	129	129	93	136	37	177	8	12	327
121	33	72	46	68	45	75	123	113	36	89	15	8	327
	37	75	50	68	49	80	123	123	37	89	20	6	393
122	37	113	83	93	50	70	89	80	36	96	18	9	327
	42	118	108	108	60	80	104	96	45	104	24	10	365

G = Gamma values or relative intensity.
* = See table 1 for other data on same samples.

TABLE 3

Elements in white pine needle samples from E. L. Stone, Professor Forest Soils, Cornell University. Plot B–22, 19 year old, sampled October 31, 1953

Sample No.	1953 growth	Needle tips cm	B 2498 G	Si 2507 G	P 2536 G	Mg 2779 G	Mn 2801 G	Pb 2833 G	Fe 3020 G	Al 3093 G	Ca 3159 G	Cu 3274 G	Ag 3280 G	Zn 3282 G	K 4044 G	Li 2741 G
236	Apical 2 cm	0–.5	117	167	28	32	108	22	83	356	20	43	19	13	8	53
			142	158	24	31	104	20	80	333	18	43	18	12	9	52
237	Apical 2 cm	.5–1.0	75	72	24	37	100	21	100	200	24	47	16	14	10	53
			62	62	22	37	93	22	89	182	22	46	17	12	10	55
238	Apical 2 cm	1.0–	28	20	30	59	72	22	38	142	22	22	13	12	12	57
			22	17	24	52	64	29	34	129	19	25	14	12	12	62
239	Basal 5 cm	0–.5	50	149	26	31	93	20	89	356	18	47	14	10	7	53
			39	136	24	31	96	21	104	327	17	52	14	10	7	57
240	Basal 5 cm	.5–1.0	31	41	24	32	93	18	46	158	22	43	14	11	11	64
			24	35	18	29	83	17	42	158	20	39	14	10	12	64
241	Basal 5 cm	1.0–	22	28	30	44	66	17	43	123	20	22	12	11	12	57
			15	22	22	39	60	20	36	118	18	27	11	12	12	62

G = Gamma value or relative intensity.
Spectrographic Plate No. 27, Book No. 11, David Chou.

TABLE 4

White pine needles, near greenhouse, Ohio Agr. Expt. Station May, 1955

	B 2798 G	Si 2881 G	Fe 3020 G	Al 3093 G	Mn 4035 G	Mg 2802 G		Li 2741 G
Tip 1	108	136	104	248	96	80		72
2	24	41	64	86	83	86		75
3	10	50	68	104	68	96		104
Base 4	5	35	46	70	35	64		104

	P 2536 G	Pb 2833 G	Ca 3178 G	Cu 3274 G	Na 3302 G	Ag 3280 G	Zn 3282 G	K 4044 G
Tip 1	14	26	12	37	12	7	6	32
2	8	30	18	39	16	7	5	41
3	11	41	32	53	20	12	8	64
Base 4	8	33	35	53	22	12	8	66

Spectrographic Plate No. 52, Book No. 11, A. R. Correll.

Accuracy and expression of results. Spectrographic analyses can be very accurate for certain elements, especially when these are present in very small amounts. The National Bureau of Standards accepts the spectrographic results over chemical results in many instances where only small amounts are involved. In most of the work reported in this paper only large differences in concentration are discussed.

The results of spectrographic analysis can be expressed just as any other analysis, in percent or parts per million, but sometimes this is very difficult because

of the very small amounts involved. It is often better to express the results in comparative amounts rather than in absolute values. One should know the copper constant of an ore very accurately; but since all biological material contains a little copper, it is often more important to know the relative amount of copper in one tissue as compared to another than to have the absolute amount in each. And it is much easier to do this.

Starting with the spectra of a series of plant samples on a spectrographic plate, one can first of all visually examine the density of the lines in the different spectra and see whether there is more in one than in another. Next the lines can be measured with the densitometer and compared. The values of the density measurements can be corrected for emulsion response, and for spectrogram variations (internal standard), and further compared. The values can be expressed in absolute amounts in the sample mixture from prepared working curves. Finally, if the ash content of the dried tissue is known, they can be expressed in amount per unit of dry tissue and if moisture were determined on the wet plant tissue, then in amounts in the wet tissue.

RESULTS

This work, resulting from a rather extensive program on the study of mineral elements in the margins and tips of corn leaves, has been extended to many other plants such as sorghum, sugarcane, wheat, oats, grass, iris, lily, wheat awns, and pine needles.

Only the results on pine needles are discussed here. The samples were obtained from New York State through the kindness of E. L. Stone at Cornell and from the campus and arboretum here. Several graduate students and technicians besides myself have worked on the samples.

The results of the boron analyses in the first set of samples from New York State are tabulated in table 1 in some detail to show how is it done. These data show the high accumulation of boron in the tips of needles.

Table 2 shows the results of spectrographic examination of the same set of samples for eleven other elements besides boron. These data are summarized as gamma values or relative intensities only to save space. They show that, in addition to boron, silicon, manganese, iron, copper, and aluminum are higher in the tips than in the rest of the needle. Phosphorus, magnesium, lead, calcium, silver, or zinc, show no difference; potassium is slightly lower in the tips than in the other parts of the tissue.

The data in table 3 show the elements examined in white pine needles. The sample size was too small for a 90–10 buffer mixture, so a mixture of 100 milligrams of LiF and 100 milligrams of tissue were used. The results are recorded in relative intensities and they show a high accumulation of boron, silicon, aluminum, manganeses, iron, and copper in the tips and about equal amounts of the other elements throughout the needle, with the exception of potassium which is lower in the tips.

A set of white pine needle samples was obtained by Tzu-liang Yuan at Wooster and separation or dissection made into 4 parts. These samples were put on Plate No. 52 by A. R. Correll and the results are shown in table 4. Here again there was an accumulation of boron, silicon, aluminum, iron, and manganese in the tips of the needles, with six of the elements about equally distributed in the needle, and potassium again lower in the tips then elswhere.

SUMMARY

It appears from these studies on pine needles that boron, silicon, manganese, aluminum, iron, and copper accumulate in the tips; that phosphorus, magnesium, lead, calcium, silver, and zinc are uniformly distributed and that potassium is lower in the tips and high in the base of the needle.

MYCORRHIZAE OF TREES WITH SPECIAL EMPHASIS ON PHYSIOLOGY OF ECTOTROPHIC TYPES

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Most absorbing roots of forest trees in their native habitats are invaded by specific nonpathogenic fungi; together the roots and fungi comprise very orderly morphological units, the mycorrhizae. Physiologically, mycorrhizae represent cases of symbiosis, or reciprocal parasitism, but not of pathogenesis. To give an insight into our present knowledge of the physiological interactions of trees and mycorrhizal fungi, I shall first discuss briefly some of the morphological characteristics of mycorrhizae.

CLASSES OF MYCORRHIZAE

On the basis of the interrelation between the fungus hyphae and the root cells, mycorrhizae are classed in two main groups, ectotrophic and endotrophic. The kind is usually specific for a tree genus. Typical ectotrophic mycorrhizae are caused by invasion of actively growing absorbing roots usually by hymenomycetous, but sometimes by ascomycetous, fungi. These fungi usually form compact mantles of mycelium on the surface of the roots. Subsequently they dissolve the middle lamellae of the epidermal and outer cortical cells and then the hyphae surround the walls of those cells. The living epidermal and cortical cells are thus isolated by mycelial partitions. The diameters of the invaded roots are increased, but the cell volumes are not changed. In sectioned material the pattern formed by hyphae in the cortex is referred to as the Hartig net. The meristematic tip and the stele of the root are not invaded by hyphae. The infected roots are shorter than those uninfected, sometimes are branched, and do not develop root hairs. Ectotrophic mycorrhizae are commonly found on pine, spruce, oak, elm, beech, hickory, chestnut, birch, and other trees.

Endotrophic mycorrhizae are caused by the invasion of absorbing roots by specific phycomycetous fungi. The hyphae are present on the root surfaces only as individual threads and penetrate directly into the root hairs and other cells of the epidermis. Penetration of cells sometimes extends no farther than the epidermis; frequently, however, the hyphae grow into the cortex cells. Within the cells the hyphae may appear as coils, swellings, or minute branches. As in ectotrophic mycorrhizae, there is no penetration of meristem or stele. The gross morphology of the invaded roots may remain unchanged or the roots may become beaded, the beading probably being caused by periods of arrested growth of the roots followed by periods of active growth as the result of changes in environmental conditions. Endotrophic mycorrhizae are commonly found on yellow poplar, maple, sweet gum, and ericaceous plants.

Besides the two types of mycorrhizae just described, there occasionally appears on tree roots the typical organization of the ectotrophic mycorrhizae plus intracellular penetration by hyphae. These ectendotrophic mycorrhizae are sometimes thought to represent a transitional stage between the ectotrophic and the endotrophic type but may represent either a pathogenic tendency on the part of an ectotrophic fungus under conditions unfavorable to the host or a secondary invasion by fungi of a weakly parasitic nature brought on by alterations in the rhizosphere.

Sometimes invasions by pathogenic fungi may change the gross morphology of absorbing roots so that they appear similar to ectotrophic mycorrhizae. Hyphal penetration, however, is not restricted to specific tissues and ultimately results in

death of the roots. Sometimes referred to as pseudomycorrhizae, these are clearly cases of pathogenesis detrimental to the host.

FORMATION OF MYCORRHIZAE

Investigators of the physiology of mycorrhizal associations have long sought to learn their significance and understand the mechanisms involved. From the results of many isolated experiments in different parts of the world it is now possible to synthesize a reasonable, partial explanation of the mechanisms of the association.

The first requisite for the formation of mycorrhizae is, of course, contact between actively growing roots and compatible fungi. The contact may originate from spores germinating in the vicinity of the roots, by extension through the soil of hyphae from either residual mycelium or established mycorrhizae, or by progression of hyphae through internal root tissues. Thereafter many inter-actions are initiated between the fungi and the root cells.

Growth of mycorrhizal fungi on the surfaces of the roots is greatly stimulated by exudates from the roots. These exudates contain at least one growth-promoting metabolite, which the discoverer designated as the M-factor. This substance has not been identified, but it is not any of the known B vitamins, the purine and pyrimidine bases or the amino acids in casein-hydrolysate. Dependency on the M-factor varies widely with the various species of mycorrhizal fungi. Use of the metabolite will probably greatly assist in culturing mycorrhizal fungi which have resisted all attempts at isolation and maintenance in pure culture.

Entrance of ectotrophic mycorrhizal fungi into the roots requires secretion of pectolytic enzymes, which dissolve the middle lamellae and thus permit the hyphae to grow through the intercellular regions of the cortex. Endotrophic mycorrhizal fungi secrete cellulolytic rather than pectolytic enzymes. By penetrating the cell walls the hyphae enter the intracellular regions of the cortex cells. Fungi which cause ectendotrophic mycorrhizae secrete both pectolytic and cellulolytic enzymes. Physical or chemical properties of the roots, or perhaps both, restrict the hyphae of all mycorrhizal fungi to the cortex delimited by the endodermis and meristematic cells of the root tip. The mechanism of this resistance to the hyphae is not known.

The growing, absorbing roots of several species of forest trees which have become enveloped by ectotrophic mycorrhizal fungi are subjected to a growth-regulatory substance, which may be indoleacetic acid. This substance causes modification of subsequent root growth. It retards elongation of the roots and frequently initiates dichotomous branching. The end result may be very dense coralloid formations of mycorrhizae. The cortex cells are oriented somewhat differently from those in non-mycorrhizal roots, and presence of intercellular hyphae causes a swollen appearance. There is, however, no increase in the cell volume. It is probable that formation of new absorbing roots is initiated by the growth-regulator. When root systems of responsive species are placed in liquid culture media or extracts thereof, branching occurs even without mycorrhizal formation. The branched absorbing roots and the mycelium radiating from the surfaces of mycorrhizae greatly increase the absorbing potentiality of any particular mycorrhizal root. Trees with endotrophic mycorrhizae apparently do not respond to the secretions of the growth regulator. This leads us to believe that trees having ectotrophic or endotrophic mycorrhizae are different physiologically and that this inherent difference determines the type of mycorrhizal association into which the species will enter.

EFFECTS OF SOIL ENVIRONMENT

Soil Acidity

Mycorrhizae of trees develop most extensively in acid soils, probably because all mycorrhizal fungi of trees studied for pH requirements are acidophilic. However, different species have different optima for maximum growth.

Organic Growth Factors

Several other soil factors besides acidity strongly affect development of tree mycorrhizae. There is evidence that certain vitamins and amino acids, for which mycorrhizal Hymenomycetes and Gasteromycetes are heterotrophic, are available in the soil in sufficient amounts for maximum growth of the fungi. These may originate as products of the metabolism of other microorganisms during decomposition of organic matter. There is also evidence that substances inhibitory to mycorrhizal fungi are produced by microorganisms in the soil and that other inhibitors are present in leaf litter of aspen, beech, maple, oak, and pine.

Temperature, Aeration, and Moisture

The greatest frequency of mycorrhizal formation is during the spring. Formation then decreases in early summer, but there is a second peak during early autumn. Abundance of new mycorrhizae may be correlated with higher soil moisture levels during spring and autumn as compared with those in summer, when rainfall is less and transpiration rates are high. Low temperatures during mid-winter limit the development of mycorrhizae by suppressing root and fungus growth. In late winter and very early spring while the shoots of trees are apparently dormant, roots may grow extensively and be invaded by mycorrhizal fungi. Thus, by the time the buds begin to swell, the roots are in a very active state.

For good development of mycorrhizae soils should be well aerated. Heavy clays reduce root and fungus growth by decreasing aeration while light-textured soils may do the opposite. The balance between soil moisture, aeration, and temperature can determine the complement of microorganisms and in all probability the species of fungi which will enter into the state of mycotrophy under a given set of conditions. More attention should be given to those factors as they influence formation and physiological activity of mycorrhizae.

Nutrient Level

The available inorganic ions in the soil have a profound effect on mycorrhizal formation if all other factors are optimal. The results of several investigators consistently show that formation of ectotrophic mycorrhizae varies inversely with soil fertility. This appears to be especially true when related to the available phosphorus, nitrogen, and potassium in the soil. In soils which accumulate large amounts of humus and consequently have low amounts of soluble nutrients, mycorrhizal formation is most profuse and the mycorrhizae are most effective in stimulating the growth of trees. When decomposition of humus is rapid and the available nutrient level high, mycorrhizal formation is relatively less. Addition of inorganic fertilizers to soils may completely suppress formation of ectotrophic mycorrhizae. Little is known as to the effects of available nutrients on formation of the endotrophic mycorrhizae.

EXPLANATION OF FIGURES IN PLATE

A. Coralloid ectotrophic mycorrhizae of *Pinus virginiana*.

B. Cross-section of an ectotrophic mycorrhiza of *P. virginiana* illustrating intercellular Hartig net.

C. Beaded form of endotrophic mycorrhizae of *Acer rubrum*.

D. Longitudinal section of an endotrophic mycorrhiza of *A. rubrum* illustrating intracellular hyphae.

E. Seedling of *Pinus virginiana* grown aseptically on a vermiculite substrate.

F. Cross-section of an ectendotrophic mycorrhiza of *P. strobus* illustrating Hartig net and intracellular hyphae.
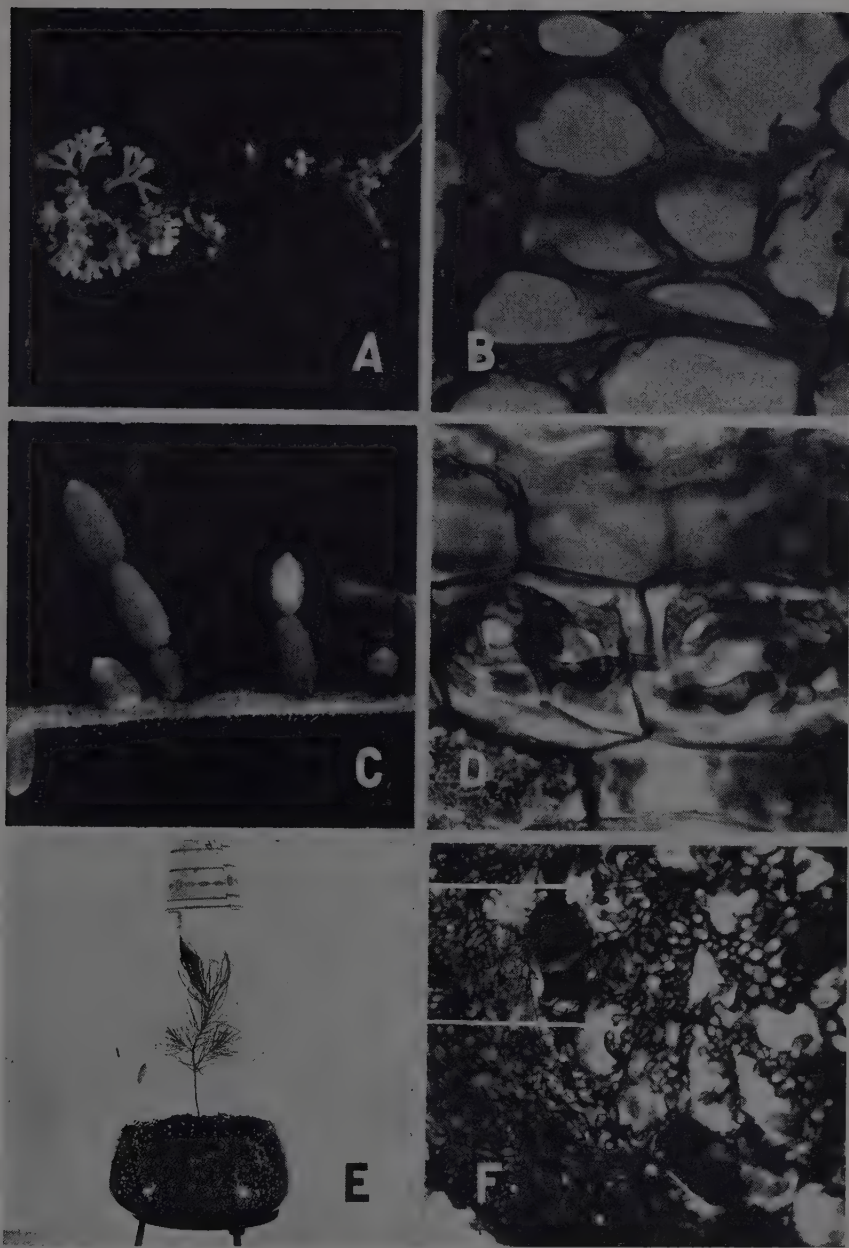
MINERAL NUTRITION

The earliest indications that ectotrophic mycorrhizae were of benefit to trees appeared in experiments wherein seedlings growing in soils devoid of mycorrhizal fungi ceased growth after one or two years. When other seedlings with mycorrhizae were interplanted in the beds, the fungi spread through the soil and invaded the uninfected roots. Thereafter vigorous renewed growth occurred on the retarded seedlings. Similar results were obtained by inoculating the beds with duff containing mycorrhizal fungi. Chemical analyses of plant tissues have shown that plants with mycorrhizae may contain as much as 86 percent more nitrogen, 234 percent more phosphorus, and 75 percent more potassium than those without mycorrhizae. In recent years radioactive isotopes of several essential elements have been used to show their transfer by mycorrhizal fungi from the substrate into roots and their translocation throughout the plant. Mycorrhizae also accumulate greater amounts of phosphorus than do short roots with root hairs. This accumulation is closely related to the respiration of mycorrhizae.

INFLUENCES OF LIGHT

The effects of light on mycorrhizal formation are manifested indirectly as a result of the response of the host to light intensity. Formation of mycorrhizae may be reduced or completely suppressed on plants grown under low light intensities. Girdling of stems, which results in interrupting translocation of carbohydrates to the roots, inhibits mycorrhizal formation. This is correlated with the amount of carbohydrates in the roots and subsequently with the effects of the carbohydrates on the nutrition of the fungi. Logically, species requiring high light intensities should be at a disadvantage as regards mycorrhizal formation if grown in the shade. There is little evidence to date that variation in photoperiod influences formation of mycorrhizae.

STATUS OF CURRENT KNOWLEDGE AS TO RECIPROCAL EXCHANGES IN MYCORRHIZAE

From experimental evidence thus far obtained one may assume the following regarding the reciprocal effects of roots and ectotrophic mycorrhizal fungi. Accumulation of soluble carbohydrates in the roots of trees in some instances depends largely upon light intensity and duration and favors secretions of a growth-stimulating metabolite into the rhizosphere. Mycorrhizal fungi, usually Hymenomycetes or Gasteromycetes, present in the rhizosphere are stimulated by the metabolite and invest actively growing short roots. Secretions of an auxinlike compound by the fungi cause the absorbing roots to develop into short, sometimes profusely branched structures, especially on pines. Secretions of pectolytic enzymes enable the fungus to enter the intercellular regions of the cortex only. Restriction of hyphae to the cortex and the entrance of specific fungi into the roots are controlled by unknown mechanisms. The hyphae, which frequently radiate some distance into the soil adjacent to the roots, absorb and translocate nutrients from the soil into the root tissues in greater quantities than do roots without mycorrhizae. In exchange, the fungi utilize carbohydrates and probably other growth substances from the root cells. This exchange may be altered by several environmental factors including the available nutrients in the soil and the light intensity.

Fertilizers added to the soil are readily absorbed by the tree. When they are translocated upward near the source of the photosynthate, soluble carbohydrates are assimilated rapidly during formation of new protoplasm and cell walls in the shoot. The amounts of soluble carbohydrates translocated to and accumulated in the roots, and of the M-factor secreted, would be low. Formation of mycorrhizae would not be favored under these conditions. Reduction in light intensity would

not favor shoot growth but would result in a similar low amount of soluble carbo-
hydrates in the roots and would suppress mycorrhizal formation.

Since little more than morphological studies have been made on the endothropic
mycorrhizae of trees, the physiological aspects of the relationship are not well
established. It has been observed, however, that hyphae which invade the root
cells follow the advancing meristematic root tip and grow from cell to cell. The
older hyphae are then digested by the root cells and probably the contents of the
hyphae are assimilated by the host. Cytochemical studies may be used in the
future to assist in determining the physiological interactions.

PRACTICAL APPLICATIONS

Seed of some species of trees introduced into certain parts of the world must
be complemented with suitable mycorrhizal fungi which are not indigenous there.
This may be accomplished by starting the seedlings in beds into which mycorrhizal
fungi have been introduced. Interplanting with seedlings having mycorrhizae
is effective also. In Sweden it is recommended that fertilizing of the seedlings
should be done sparingly if the trees are to be transplanted where they will not
be fertilized. In this country it would also seem advisable to encourage a good
mycorrhizal system before transplanting; high rates of application of fertilizer
produce larger stocks but few mycorrhizae and later, when the plants are becoming
established, difficulties may result.

When seed beds are being prepared, it is now common practice to control
soil pathogens by application of chemicals to the soil. Some chemicals may cause
stunting of the seedlings by direct injury to the plants. Others, when used in
high concentrations, can eliminate both soil pathogens and mycorrhizal fungi.
The reduction of competition for soil nutrients results in larger seedlings. It
would be advisable under such conditions to inoculate the beds with mycorrhizal
fungi to permit formation of mycorrhizae prior to transplanting. Other chemicals
may reduce the population of organisms and prevent serious losses of seedlings
but do not kill enough of the mycorrhizal fungi to prevent their redistribution in
the seed bed and on the roots. The soil treatments most widely used at present
seem to do the latter.

TRENDS OF INVESTIGATIONS

Physiological studies of mycorrhizae, though complicated and requiring the
development of new techniques, should be performed both under controlled
laboratory conditions and in the field to clarify further the functions of mycorrhizae.
The place of endotrophic mycorrhizae in successful nutrition of some trees and
the effects of pH, soil nutrients, light and other factors on their formation should
be determined. Our lack of knowledge about endotrophic forms leaves much
to be investigated.

Fungi forming ectotrophic mycorrhizae are known to vary in their physiological
requirements and therefore may be expected to vary in their efficiency as partners
in the mycorrhizal associations. Research designed to select the most efficient
fungus associates of the various tree species for use in various soil types is indicated.

In preliminary experiments we found indications that the auxin effects on
root systems vary with species of trees depending upon whether the mycorrhizae
are ectotrophic or endotrophic. There is indicated the need for basic studies on
the differences between roots of trees in their responses not only to ectotrophic
and endotrophic mycorrhizal fungi but to other root invaders.

Synthetic growth-regulators can probably be used to initiate new roots on
transplants if a practical method is devised for treating them. Such seedlings
inoculated with mycorrhizal fungi should be in a better condition for survival than
uninoculated ones. In preliminary studies, new roots were initiated on pine

seedlings and converted to mycorrhizae when indoleacetic acid and pure cultures of mycorrhizal fungi were used.

It would be of interest to know whether the fungi secreted metabolites of an antibiotic nature which might retard growth of other soil organisms as well as affect the metabolism of the host.

Controlling diseases by use of biocides in soil treatments and of systemic protectants is a goal of plant pathologists. We know that the soil treatments do affect mycorrhizal fungi. We now wonder whether it would be possible to reduce greatly the microflora and fauna in the soil, permit the tree seedlings to become established under conditions of reduced competition for nutrients, and then inoculate the seed beds with pure cultures of the most efficient mycorrhizal fungi. It will of course be necessary first to screen the fungi for relative efficiencies. In any case we hope that the mycorrhizal association will not be overlooked so that latent damage by biocides to the absorptive systems will not exceed the initial benefits from control of disease and reduction of competition.

In conclusion, one might state that a given tree species will grow if climatic and soil conditions permit. However, growth will be best when biotic conditions, and especially the natural development of the mycorrhizal association, are best. Better growth can be obtained if biotic relations are worked out through studies of mycorrhizae and the principles are applied to practical problems.

DISCUSSION

WM. H. DAVIS MCGREGOR (*U. S. Forest Service and Duke University*): Do you have any evidence that the micorrhizal fungi produce indoleacetic acid?

EDWARD HACSKAYLO: The growth-regulatory substance which causes dichotomous branching of ectotrophic mycorrhizae has not been specifically identified as indoleacetic acid. We do know, however, that at least one species of *Boletus* does produce indoleacetic acid and that other fungi may secrete organic acids including indoleacetic acid. At present we are assuming that this is the substance causing the morphological changes.

DENNIS RICHARDSON (*University of Aberdeen, Scotland*): I do not believe we have any evidence of a fundamental difference in root physiology between trees which form ectotrophic mycorrhizae and those forming endotrophic association. Such a difference has been adduced from the fact that the formation of uninfected roots closely resembling mycorrhizae can be produced as a result of adding auxin to the growth medium in the case of ectotrophic forms, but not in that of endotrophs. This is true, but there is evidence in the case of *Acer* that such roots can be produced by the addition of auxin to the terminal shoot of a decapitated and defoliated seedling.

It was also suggested that there is a difference in root physiology because, *e.g.*, ectrophic mycorrhizal fungi do not infect roots of endotrophic trees and if there were no difference dual infection should be possible. This, I think, is a dubious conclusion; could it not be that the difference lies in the fungi (which are known to differ in *e.g.* the enzymes they secrete) rather than in the roots? Or be due to differences in environmental requirements between endotrophic type roots and ectotrophic type fungi?

EDWARD HACSKAYLO: Species of trees which have either ectotrophic or endotrophic mycorrhizae are frequently found growing adjacent to each other. The fungi involved in each of those associations are present in the soil and yet maintain specificity in the root penetrations. Why then do not the fungi which cause ectotrophic mycorrhizae and secrete pectolytic enzymes penetrate roots of trees which are invaded by only the cellulolytic enzyme-producing fungi? I am more inclined to believe that it is a host-resistance to the fungi which points toward a physiological diversity in the tree species. If differences in environmental require-

ments are involved this would again strongly suggest that the differing responses of the hosts to a given environment has a physiological basis.

DENNIS RICHARDSON: Would you agree with the contention first stressed by Harley that mycorrhizae cannot be regarded as unique examples of plant-microorganism inter-relationships? That, in fact, a mycorrhiza is just one of many such associations between a plant root and a component of the rhizosphere population?

EDWARD HACSKAYLO: Certainly mycorrhizae are very widespread and I would be the first to acknowledge that they are only one component of a complex population of micro organisms in the rhizosphere which must be exerting influences on each other and on the higher plants.

A. G. SNOW (*U. S. Forest Service*): You mention complete separation of cortex cells by Hartig net. Are there any cyto-protoplasmic strand connections also between these cortex cells?

EDWARD HACSKAYLO: We do not know whether there might be connections similar to plasmodesmata between the cortex cells. Possibly stain techniques could be used to establish the answer to that question.

LIGHT EFFECTS ON TREE GROWTH AND SEED GERMINATION

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Everyone knows that trees cannot grow without light, but not *why* they require light for processes besides photosynthesis. What are some of these effects of light on trees and why are they not more widely recognized as light effects? What is the nature of the reactions in plants that make them responsive to light? These are among the questions with which we are concerned.

Photoperiodic Growth Response in Trees

Perhaps one of the most conspicuous effects of light on trees is expressed in photoperiodic control of their growth. Seedlings, rooted cuttings or young plants of many woody species continue growing or stop growing in response to long or short days, respectively. This is a conspicuous response observed and mentioned by Garner and Allard (1920) as a daylength effect, but still not widely recognized as such. Stoppage of growth is frequently attributed to low temperature, but it occurs in many species before temperatures decline.

If woody plants are grown in the greenhouse on different photoperiods but with other environmental variables held constant or varied the same for all daylengths, their photoperiodic response is quickly apparent. A great many species stop growing almost immediately if subjected to daily photoperiods of 8, 10, or 12 hours even though the temperature is not limiting. Most of these same species grow for much longer periods, and some of them indefinitely, on photoperiods of 16 or more hours per day. Such results are obtained under conditions of essentially equal light energy regardless of differences in daily light duration. Differences in photosynthesis are thus excluded as the cause of the differences in response.

Effects of Short Photoperiods on Growth

When trees are subjected to photoperiods short enough to stop growth of their shoots, one of the first effects is a decrease in elongation of newly formed internodes

(Downs and Borthwick, 1956b; Downs, 1957). Simultaneously, the plant develops resting buds typical of its kind. In some species, such as *Liriodendron tulipifera* L. and *Betula mandshurica* (Regel) Nakai, this entails no important structural modification of the foliar primordia produced by the terminal meristem because no bud scales are formed. The stipules perform the function of scales and so the formation of a bud by such a plant results from almost complete stoppage of elongation of newly formed internodes, suppression of development of newly differentiated leaf primordia and probably a lowering of the rate of differentiation of new primordia.

In other species, such as *Liquidambar styraciflua* L., the buds are enveloped by bud scales. This means that one of the first evidences of bud formation is the production of scale primordia by the terminal meristem. When photoperiodic conditions are such that bud formation occurs, the meristem produces many bud scales and then resumes the production of primordia of normal foliaceous leaves. As in *Liriodendron*, the elongation of internodes is reduced to a minimum and the rate of production of new structures appears to slow down. In some of our day-length experiments a few *Liquidambar* trees initiated two or three bud scales in response to one of the daylength treatments, but then they resumed the production of typical foliage leaves without proceeding further with the formation of a bud. These sporadically formed bud scales remained attached at their respective nodes for a time and became separated from each other by internodes of appreciable length.

In still other species such as *Catalpa bignonioides* Walt. and *C. speciosa* Warder, cessation of growth in response to short days is accomplished by abscission of the terminal. One of the first observed effects, however, is again suppression of elongation of newly formed internodes. One of these internodes presently begins to blacken and soon it is abscised, carrying with it the entire stem apex. When growth is resumed, it occurs from axillary buds. Thus, growth of *Catalpa* is sympodial (fig. 1).

Growth on short days continues for many weeks in species such as *Ulmus americana* L. but eventually ceases. Other woody plants such as *Pyracantha coccinea* Roem. seem to grow as well on short days as on long ones. Certain woody plants from the Tropics are as responsive to daylength as many of those from the temperate zone. *Rauvolfia vomitoria* Afzel. and *Theobroma cacao* L., for example, grow more vigorously on 16-hour days than on 8- and 12-hour ones, a point of special interest because in the Tropics daily durations of light as great as 16 hours are never encountered in nature. On 8-hour photoperiods neither of the species stopped growing completely during the several month period of the test, but the rates were very low.

Although short-day treatments result in stoppage of terminal growth of shoots of a great many trees, they retain their leaves in most cases for many months. The leaves of such trees generally become chlorotic and may exhibit minor structural malformations similar to those of trees suffering from nutritional disturbance. Unbalanced nutrition may, in fact, be a secondary effect of short-day treatments. We have observed that the addition of fertilizer to *Cornus florida* L. in amounts fully acceptable on long-day treatments results in the quick death of the trees on short days.

Temperature operating directly or interacting with light is also effective in stopping length growth of trees, but our own experiments have not yet examined this possibility extensively. Such an effect could be one in which temperature changes the responsiveness of the plant to light, or temperature might operate through completely different pathways. It is sufficient, where the emphasis is on light and its mode of action rather than on final response, to point out that in woody, as in non-woody plants, a photoreaction controls growth. This photo-reaction expresses itself through the photoperiodic mechanism, and is thereby

identified with the photoreaction controlling flowering. It also expresses itself through wide non-photoperiodic responses, which will be presented after further effects of photoperiod on tree growth are described.

Maintenance of Continuous Growth

Trees such as *Cornus florida* and *Acer rubrum* L. (Downs and Borthwick, 1956b) and shrubs such as *Weigela florida* var. variegata (Bean) Bailey (Downs and Borthwick, 1956a) can apparently be kept in a continuous state of shoot elongation

FIGURE 1. *Catalpa bignoniodes* grown on 8– and 16–hour photoperiods. Left: **23** weeks of 8–hour photoperiods. Center: 8 weeks of 16–hour followed by **15** weeks of 8–hour photoperiods. Right: **23** weeks of 16–hour photoperiods.

if they are constantly subjected to long-day treatment and the elongation can be stopped abruptly by short-day treatment. Other kinds of woody plants such as species of *Pinus* and *Quercus*, however, stop growth and form terminal buds even though long photoperiods are maintained continuously. After a period of inactivity the buds break, new flushes of leaves are produced and again buds are formed. This type of growth has been observed to persist in these genera for

several months under experimental conditions in the greenhouse. In nature the growth of these plants follows a similar pattern except that in some species a single flush and in others only two occur in a year. The inhibitory effect of the shortening summer days could obviously account for the lack of additional flushes of growth, but the possible inhibitory effects of other factors are not excluded.

The daily duration of light required to maintain growth of woody plants varies widely with the species. For several a sharp change in effect from inhibition to promotion of growth occurs when the daylength is increased from 12 or fewer hours to 14 or more hours per day. For others such as *Aesculus hippocastanum* L. no duration of light, including continuous, prevents early cessation of growth, but *Aesculus* makes appreciably more growth on long photoperiods than on short ones.

Conditions Including Resumption of Growth

Growth of a woody plant stopped by short photoperiods can sometimes be made to resume by subjecting the plant to long photoperiods. Examples are *Weigela* and *Cornus*. Others such as *Catalpa* and *Aesculus* require a few weeks of low temperature, whereas defoliation is adequate for trees such as *Paulownia*, especially if they are simultaneously given continuous light. *Weigela* will resume growth even on short days if defoliated, but as soon as the new shoots are formed their further growth is inhibited by the short photoperiods. While short-day treatment is thus an effective means of stopping growth of many trees, long-day treatment is not an assured means of either maintaining growth or inducing its resumption. Its effectiveness depends on the kind of plant and on conditions other than light.

Tree Growth as Influenced by Light Quality

Another aspect of light responsiveness of trees is illustrated by their reactions to light from incandescent-filament and fluorescent sources. Extension of a short day of natural light with either of these types of artificial light is effective in maintaining continued growth of plants such as *Catalpa*. The character of the growth, however, differs markedly, the trees receiving incandescent-filament light becoming appreciably taller than those receiving fluorescent light. In tests with *Catalpa* the average numbers of nodes produced during an experimental period of several weeks were the same, but the average internode lengths of plants receiving incandescent-filament light were twice those of ones receiving fluorescent light. This difference in effect results from differences in spectral composition of the two kinds of light and there is good evidence that the basic light reaction responsible for the difference is the same as that which makes photoperiodic control of growth of trees possible. Our knowledge of this reaction comes mainly from studies of such diverse phenomena as flowering (Borthwick *et al.*, 1952a), elongation of internodes (Hendricks *et al.*, 1956; Downs, 1955; Downs *et al.*, 1957), seed germination (Borthwick *et al.*, 1952b; Borthwick *et al.*, 1954; Toole *et al.*, 1955) and pigment formation (Piringer and Heinze, 1954; Mohr, 1957; Siegelman and Hendricks, 1957), and although not based immediately on work with trees, it is fully applicable to them.

The Photoreversible Reaction

The photoreaction responsible for so many apparently unrelated phenomena is caused mainly by red light, and the action of red is reversed by the so-called far-red wavelengths. The far-red or near-infrared region of the spectrum covers roughly the wavelength band of 7000 to 8000 Å. The wavelength regions of most effective action are about 5500 to 7000 Å for the red, with a maximum at about 6500 Å, and about 7000 to 7500 Å for the far-red reversal of the red effect, with a maximum near 7350 Å.

Specific effects of the red radiant energy are inhibition of flowering of short-day plants, promotion of flowering of long-day plants, promotion of seed germination prevention of stem elongation under certain circumstances, and promotion of the formation of certain plant pigments. Far-red radiant energy applied after red reverses these effects. Most of these phenomena are repeatedly reversible by

FIGURE 2. Effects of red and far-red radiant energy on the germination of seeds of *Pinus virginiana*. Treatments from left to right upper row—unirradiated control and 4 minutes of red; middle row—16 and 64 minutes of red; lower row—64 minutes red followed by 4 and 16 minutes, respectively, of far-red.

red and far-red and the ultimate response of the plant is determined by the kind of radiant energy used last in such a series of alternations.

Red and far-red radiant energies are obtained in very pure form by the use of a spectrograph of proper design (Parker *et al.*, 1946). They can also be had in sufficiently pure form for many kinds of experiments from ordinary lamps fitted with inexpensive filters. A suitable source of red radiant energy is a fluorescent lamp with a red cellophane filter, which removes most of the radiant energy of wavelength shorter than about 5500 Å. The fluorescent lamp is selected because it emits relatively little energy in the region from 7000 to 8000 Å. A satisfactory source of far-red energy is an ordinary incandescent-filament lamp. A filter consisting of two layers of blue and two of red cellophane effectively removes the visible light, leaving the far-red radiant energy in adequately pure form. With such sources and filters, one can perform typical reversibility experiments involving any of several kinds of responses.

The operation of this reversible photoreaction is illustrated by the control of internode length of young bean plants. The lengths attained by the second internodes of Pinto bean plants grown 8 hours per day under high-intensity fluorescent light depended on which of two kinds of radiant energy was given for a 5-minute period immediately after the fluorescent light was turned off. If the plants received far-red, the internodes became 3 to 3 and $\frac{1}{2}$ times as long as those given red at the beginning of darkness. If the plants were subjected first to far-red and then to red, the promotive effect of far-red on elongation was nullified by the red and the internodes remained as short as those of unirradiated control plants placed directly in darkness at the close of the period of high-intensity fluorescent light. The photoreversible red-far-red reaction is thus regulatory of stem length of beans.

Effects of Mixtures of Red and Far-Red Radiant Energies

One might wonder what would happen if both kinds of light were given at the same time. This is actually what generally occurs because our usual light sources emit red and far-red simultaneously but in ratios characteristic of the source. Incandescent-filament light and sunlight are kinds that contain large amounts of both, and fluorescent light also is high in red but extremely low in far-red, though not devoid of it.

If bean plants are given 8 hours of high-intensity fluorescent light followed by a few hours of low-intensity light, their internodes elongate greatly if the low-intensity source is an unfiltered incandescent-filament lamp, and almost not at all if it is an unfiltered fluorescent lamp. In this instance the plants respond to the unfiltered incandescent light as if it were almost pure far-red radiant energy. The difference in degree of elongation of *Catalpa* internodes in unfiltered fluorescent and incandescent-filament light is clearly the result of the same reaction as that in the bean.

Although *Catalpa* and bean plants respond to the radiant energy from incandescent-filament lamps as though it were predominantly far-red, some plants react to it as if it were predominantly red. Thus, incandescent-filament light, like pure red light, given in the middle of a long dark period prevents flowering of short-day plants. These plants are so much more responsive to the red than to the far-red in the mixture that they react to this unfiltered light as if it were mainly red. If one now removes the visible radiant energy, particularly the red, by the use of filters that do not remove the far-red energy, the flowering stimulus is reestablished in the plants by continuing the treatment a few minutes more with the same lamps.

Seeds of pepper grass (*Lepidium virginicum* L.) exhibit an analogous response. They germinate readily if given a few minutes of unfiltered incandescent-filament light, but their germination is reinhibited if they are covered with blue cellophane

which removes the red but not the far-red energy. Seeds of henbit (*Lamium amplexicaule* L.), on the contrary, germinate in darkness and in unfiltered fluorescent light, but their germination is prevented by unfiltered incandescent-filament light. The mixture of red and far-red in incandescent-filament light thus acts as red on *Lepidium* seeds and as far-red on *Lamium*. Germination in both plants is controlled by the same reactions, but the final response depends on the relative sensitivity of each type of seed to the opposing actions of red and far-red radiant energy.

Light Responses of Tree Seeds

Many tree seeds are light-sensitive for germination. Seeds of *Ulmus americana* (Toole *et al.*, 1957), for example, are promoted by red and inhibited by far-red. The same is true of seeds of various species of *Pinus* (fig. 2). A single brief period of irradiation with red promotes germination of a very high percentage of the seeds of *Pinus virginiana* Mill. (Toole *et al.*, 1956a), provided the temperature is held within the rather narrow limits favorable to germination, but repeated treatments frequently induce higher germination of certain other species (Toole, 1957, personal communication). This suggests that the conditions favorable to germination established by a treatment with red light are transitory and must be reestablished at daily or more frequent intervals if germination is to proceed, but other explanations are possible. For some trees brief daily treatments with light are far less effective in promoting germination than treatments for several hours per day. Seeds of *Betula pubescens* Ehrh., for example, were found by Black and Wareing (1954) to germinate much better with long daily periods of irradiation than with short ones; so they concluded that in such a case germination was a photoperiodic response. This is probably correct, and it is important to keep in mind here, as in the photoperiodic control of flowering, that the period of time measured by the seed is probably the dark time and that the function of the long photoperiod is not to increase the total radiant energy but to reduce the duration of continuous darkness each day. This is illustrated by unpublished results of Downs (personal communication) and Toole (personal communication) with seeds of *Puya berteroniana* Mez and certain species of *Pinus* in which they found that a long photoperiod induced no higher percentage germination than did a few minutes of light given at both ends of an equally long period of darkness.

CONCLUSIONS

In a brief discussion of light effects on tree growth and seed germination such as this only the most obvious ones can be mentioned. These effects, although diverse in outward manifestation, are the result of a single basic photochemical reaction. This reaction occurs very widely, probably universally, in higher plants and is also known in lower ones such as ferns and possibly others. An outstanding characteristic of the reaction that makes its identification as the cause of widely different responses positive is its photoreversibility by red and far-red radiant energies. Further characteristics are that it is saturated in either direction by very low energies and that in darkness it goes slowly from the red-saturated to the red-requiring condition. Although the light-energy requirements are low, the effects on the plants are great. This could imply that a product formed by the red or far-red treatment has characteristics of an enzyme or other energy-transferring device that participates in reactions leading to a particular response.

Although knowledge concerning the light reaction has come principally from other plants, the reaction is known to occur in trees and to be responsible for many diverse responses in them. Further study of the light reactions of trees gives promise of information important not only to our understanding of its operation in plants in general but to various other aspects of tree physiology.

LITERATURE CITED

Black, M. and **P. F. Wareing.** 1954. Photoperiodic control of germination in seed of birch (*Betula pubescens* Ehrh.). Nature 174: 705–706.

Borthwick, H. A., S. B. Hendricks, and **M. W. Parker.** 1952a. The reaction controlling floral initiation. Proc. Nat. Acad. Sci. 38: 929–934.

——, ——, ——, **E. H. Toole,** and **Vivian K. Toole.** 1952b. A reversible photoreaction controlling seed germination. Proc. Nat. Acad. Sci. 38: 662–666.

——, ——, **E. H. Toole,** and **Vivian K. Toole.** 1954. Action of light on lettuce seed germination. Bot. Gaz. 115: 205–225.

Downs, R. J. 1955. Photoreversibility of leaf and hypocotyl elongation of dark-grown Red Kidney bean seedlings. Plant Physiol. 30: 468–472.

——. 1957. Photoperiodic control of growth and dormancy in woody plants. Proc. Symposium on Tree Physiol., Harvard Forest.

—— and **H. A. Borthwick**. 1956a. Effect of photoperiod upon the vegetative growth of *Weigela florida* var. variegata. Proc. Amer. Soc. Hort. Sci. 68: 518–521.

——— and ———. 1956b. Effects of photoperiod on growth of trees. Bot. Gaz. 117: 310–326.

——— -, **S. B. Hendricks,** and **H. A. Borthwick**. 1957. Photoreversible control of elongation of Pinto beans and other plants under normal conditions of growth. Bot. Gaz. 118: 199–208.

Garner, W. W. and **H. A. Allard.** 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. Jour. Agr. Research 18: 553–606.

Hendricks, S. B., H. A. Borthwick, and **R. J. Downs.** 1956. Pigment conversion in the formative responses of plants to radiation. Proc. Nat. Acad. Sci. 42: 19–26.

Mohr, H. 1957. Der Einfluss monochromatischer Strahlung auf das Längenwachstum des Hypokotyls und auf die Anthocyaninbildung bei Keimlingen von *Sinapis alba* L. Planta. 49: 389–405.

Parker, M. W., S. B. Hendricks, H. A. Borthwick, and **N. J. Scully.** 1946. Action spectra for photoperiodic control of floral initiation in short-day plants. Bot. Gaz. 108: 1–26.

Piringer, A. A. and **P. H. Heinze.** 1954. Effect of light on the formation of a pigment in the tomato fruit cuticle. Plant Physiol. 29: 467–472.

Siegelman, H. W. and **S. B. Hendricks.** 1957. Photocontrol of anthocyanin formation in turnip and red cabbage seedlings. Plant Physiol. In press.

Toole, E. H., Vivian K. Toole, H. A. Borthwick, and **S. B. Hendricks**. 1955. Photocontrol of Lepidium seed germination. Plant Physiol. 30: 15–21.

Toole, E. H., A. G. Snow, Jr., Vivian K. Toole, and **H. A. Borthwick**. 1956a. Effects of light and temperature on germination of Virginia pine seeds. Plant Physiol. Supp. 31.

Toole, E. H., Vivian K. Toole, S. B. Hendricks, and **H. A. Borthwick**. 1957. Effect of Temperature on germination of light-sensitive seeds. Proc XI Internatl. Seed Testing Assn. 22: 196–204.

DISCUSSION *

DENNIS RICHARDSON (*University of Aberdeen, Scotland*): Is there any critical evidence that the Red-Far-Red reactions is involved in any of the known photoperiodic responses among animals as well as plants?

H. A. BORTHWICK: So far as I know there is no evidence that the photoperiodic responses of animals result from the Red-Far-Red reaction.

DENNIS RICHARDSON (in reply to a question concerning the possibility of light effects on the germination of pine having a so-called hard seed coat): Seed coats may be deceptive in their ability to transmit light. We have evidence in the case of Douglasfir that as much as 30 percent of the incident light may be transmitted by the seed coat and, when the coat is water saturated, as much as 50 percent. In view of the low light requirements of this type of response, the fact that so-called hard seed coat species respond to light cannot in my view be taken as evidence that the site of the light stimulus is in the seed coat itself. Other evidence suggests, in fact, that this is not so.

L. S. MINCKLER (*U. S. Forest Service, Carbondale, Illinois*): At what stage of germination is exposure to light effective? Apparently many species do not require such light exposure. Is that correct?

H. A. BORTHWICK: Seeds in the dry state are not significantly affected by light, but they often become responsive to light as soon as they start to imbibe water. It is true that many seeds are able to germinate in the dark. This does not necessarily mean that the light reaction does not occur in them, but it indicates that other pathways leading to germination are also present.

FOREST TREE PHYSIOLOGY RESEARCH AT THE OHIO AGRICULTURAL EXPERIMENT STATION

JOHN HACSKAYLO AND WILLIAM E. GOSLIN

Department of Forestry, Ohio Agricultural Experiment Station, Wooster

The research in tree physiology at the Ohio Agricultural Experiment Station is aimed at establishing tree responses under controlled conditions.

The area of research we are pursuing includes the establishment of the symptoms of mineral element deficiency in several tree species and the effects of day-length, light quality, temperature and humidity in seed germination and seedling survival.

The two major areas presented in this paper deal with the effect of day-length on foliar abscission in several deciduous species and the effect of light quality on winter chlorosis in Scotch pine (Riga).

Effects of Day-length on Foliar Abscission in Several Species of Deciduous Trees

In a field experiment it was found that under total darkness the leaves of black locust abscissed by 15 days and those of red oak and white ash by 21 days. Under a 4-hour day-length there was no abscission in black locust; however, in the case of white ash and red oak at 56 days 70 percent and 90 percent of the leaves had abscissed, respectively. Longer photoperiods had no effect upon abscission in any of the above species.

The findings of the field experiment indicated that there was a differential reaction between species to day-length, and a more intensive study was set up under greenhouse conditions.

METHODS

On September 27, 1956, plants of the following species were potted and placed under greenhouse conditions: white ash, black locust, sugar maple, tuliptree, red oak, white oak, and redgum. The plants were initially maintained under a 15-hour day length, kept well watered, and observed daily as to changes in leaf color and leaf fall. On October 26, 1956, three plants of each species were placed in black cloth chambers on greenhouse benches under the following day-lengths: 0; 15 min.; 30 min.; 1 hr.; 2 hr.; 4 hr.; 15 hr.; and 24 hr. The 8-hour day-length period was omitted based upon field results in that no foliar abscission occurred.

The daily temperature ranged between 70 and 80 degrees F and the night temperature ranged between 56 and 70 degrees F.

RESULTS

The results are presented using averages and since the 15-min. and 1-hour photoperiodic reactions were intermediate between the 0 and ½-hour and ½-hour and 2-hour periods, they are omitted from the graphs.

Black locust.—Black locust responded to the narrowest range of day-length in that foliar abscission occurred during the 0 to 1-hour photoperiods. At 0 hours 100 percent leaf abscission was evident at 12 days and at 1 hour, 32 days. By 36 days only 14 percent of the leaves abscissed under the 2-hour period and 17 percent under the 4-hour period, while the plants continued to grow and no leaf fall occurred under the 15- and 24-hour period (fig. 1 and 2).

The leaflets abscissed prior to the petioles and under the 0 to 30 minute period

leaves remained green. Epinasty and anthocyanin pigmentation were evident in the leaves under the 1-hour photoperiod and yellowing of the top leaves in 2 and 4-hour periods (fig. 2).

Tuliptree and sugar maple. Both the tuliptree and sugar maple responded in a very similar manner and only the data on the tuliptree are presented.

The range of reaction of foliar abscission was from 0 to 2 hour day-length, with 100 percent foliar abscission at 32 days under 0 hours; 100 percent abscission under $\frac{1}{2}$ hour; 74 percent abscission under 2 hours; 34 percent abscission under 4 hours; and 8 percent abscission under 15 hours at 36 days (fig. 1 and 2).

The lower leaves were normally first to abscise and prior to abscission turned a bright yellow color.

The plants under the 15- and 24-hour period were a good green color and continued to produce new leaves.

Red oak.—Red oak was similar to the tuliptree in reaction, but the rate of abscission was earlier and higher. One hundred percent abscission occurred at 28 days under 0 hours day-length; 90 percent under $\frac{1}{2}$ hour at 32 days; 86 percent under 2 hours at 36 days; 50 percent under 4 hours at 36 days; and 20 percent under 15 hours at 36 days (fig. 1 and 2).

The lower leaves were first to abscise, turning brown prior to abscission. In the top leaves a bright red color normally developed prior to abscission.

The plants in both the 15- and 24-hour periods remained green, but no new growth was noticeable.

Redgum, white ash, and white oak.—These three species reacted in a similar fashion as to time and rates of foliar abscission. The data on redgum are presented as being representative of the three.

The range of leaf abscission was the widest in this group, ranging from 0– to 4-hour day-length. One hundred percent abscission occurred earlier in time in white ash and white oak. The leaflets of white ash abscissed prior to the petioles, as in black locust.

In redgum, 100 percent abscission occurred at 32 days under 0 hours day-length; 82 percent under $\frac{1}{2}$ hour at 36 days; 90 percent under 2 hours at 36 days; 80 percent under 4 hours at 32 days; and 8 percent under 15 hours at 32 days (fig. 1 and 2).

The lower leaves normally abscissed first. Some of the leaves abscissed green, but in general the leaves became a pale yellow color prior to abscission (fig. 2).

The plants under 15– and 24-hour day-length periods appeared to continue to grow in that new leaves were produced during the experiment.

CONCLUSIONS

Under the conditions of this experiment, it was generally found that the rate of foliar abscission and leaf coloration was directly correlated with day-length, the rate of abscission and leaf coloration being higher and earlier under the shorter photoperiods.

Although the pattern among some species was similar, each species responded to the varying day-length somewhat differently.

Black locust had the narrowest range of reaction with respect to day-length for leaf abscission, followed in order by the tuliptree group, red oak, with the broadest range in the redgum group.

SUMMARY

1. White ash, black locust, sugar maple, tuliptree, red oak, white oak, and redgum were maintained under greenhouse conditions and day-length periods of 0, $\frac{1}{4}$, $\frac{1}{2}$, 1, 2, 4, 15 and 24 hours.

2. The temperature range was from 70 to 80 degrees F during the day and from 56 to 70 degrees F at night.

3. The plants responded in general to four ranges of day-length: 0 to 1 hour, black locust; 0 to 2 hours, tuliptree and sugar maple; 0 to 4 hours, red oak; and 0 to 4 hours, redgum, white ash, and white oak.

4. The leaflets abscissed prior to the petioles in the case of black locust and white ash.

5. Leaf coloration and rates of leaf abscission were directly correlated to day-length.
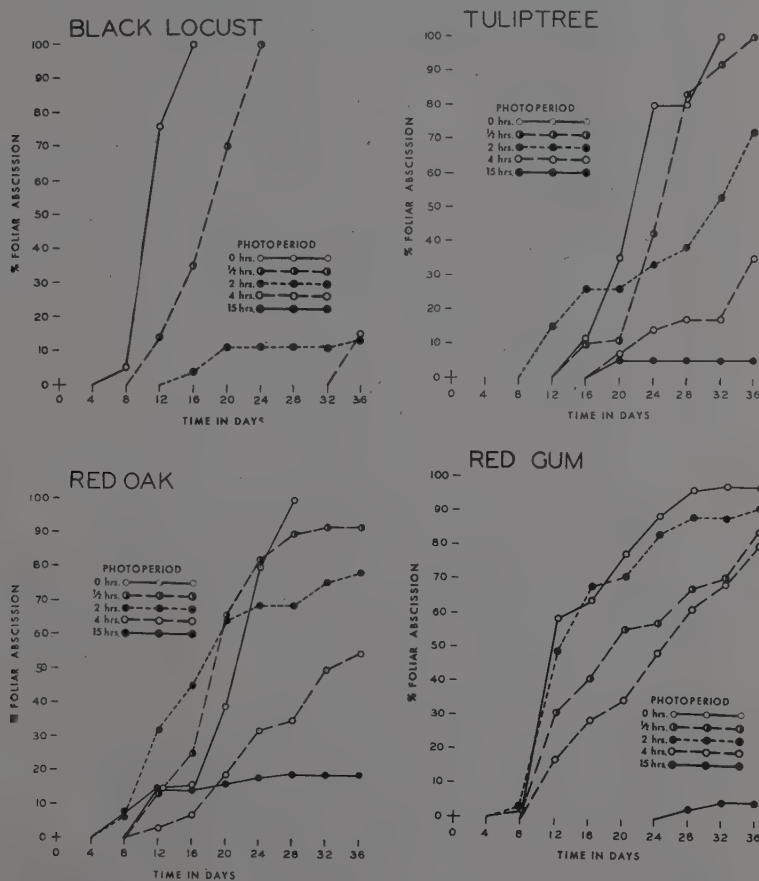
FIGURE 1. Average rates of foliar abscission in black locust, tuliptree, red oak and redgum.

The Effects of Light Quality on Winter Chlorosis in Scotch Pine (Riga)

It is known that the color of the needles during the winter months varies from a blue green to a brilliant golden yellow in Scotch pine, depending upon the origin or location of the source of seed. The problem of such winter chlorosis

has been recently reappraised due to the interest in the use of Scotch pine (Riga) in Christmas tree production.

The Riga strain of Scotch pine turns a golden yellow during late fall and early winter and was selected as the experimental plant in attempts to correct or alleviate the winter chlorotic condition.

Field applications of fertilizers in the form of single salt solutions of nitrogen, phosophorus, potassium, calcium, magnesium, and iron at the rates of 0, 100, 500, and 1000 pounds per acre did not appear to have any effect upon winter chlorosis after two years.

Spectrographic analyses of the root, stem, and leaves of a single winter collection of a yellow tree and a green tree did not indicate any appreciable differences in mineral content.   Many of the ions were of the same relative concentrations, and in some instances were higher in the yellow plant than in the green plant.

METHODS

A block of Scotch pine (Riga) planted in 1952 was selected for experimentation with the effects of the quality of light upon winter chlorosis.   The trees were a good green color on September 15; winter chlorosis was evident on October 15, and pronounced by November 15.   However, the intense golden yellow was not apparent until the last two weeks of December.

Trees were selected at random in the planting and were covered with either perforate or non-perforate polyethylene bags of the following colors: transparent, black, red, or blue.   Neither the percent of transmission nor the actual wave length transmitted have been evaluated.

The time of covering was September 15, October 15, and November 15, 1956. Each treatment was a single tree replicated twice at the above dates.   The plastic bags were removed December 15, 1956, except the September series which was removed November 15, 1956.

Visual comparisons were made of the effects of the colored polyethylene bags at two-week intervals after application.   The final evaluation was made four months after the beginning of the experiment, on January 15, 1957.

RESULTS

There were no apparent differences between the tree response to the perforate or non-perforate polyethylene bags.

September 15 treatment.—The trees covered with the transparent and blue polyethylene bags became yellow as did the uncovered trees; those covered with black died due to the probable high internal temperatures; the trees under red remained a good green color and were decidedly bluer-green than the greenest uncovered trees in the area.

October 15 treatment.—The trees under transparent, black, and blue polyethylene bags became chlorotic, while those plants under red did not become more chlorotic, but seemed to retain the color at the time of application.

November 15 treatment.—The trees responded in the same similar manner as the October 15 application.

CONCLUSIONS

Winter chlorosis of the needles apparently was not affected by the covering of Scotch pine (Riga) trees with black, transparent, or blue polyethylene bags. However, in the case of the red bags, the needles on the trees appeared to retain their green color.   Although red colored bags prevented the further development of winter chlorosis, it did not apparently result in the correction or reversal from a yellow condition to a green condition of the needles.

Further work is being prepared to observe whether this is a phenomenon of reduced light intensity or light quality.
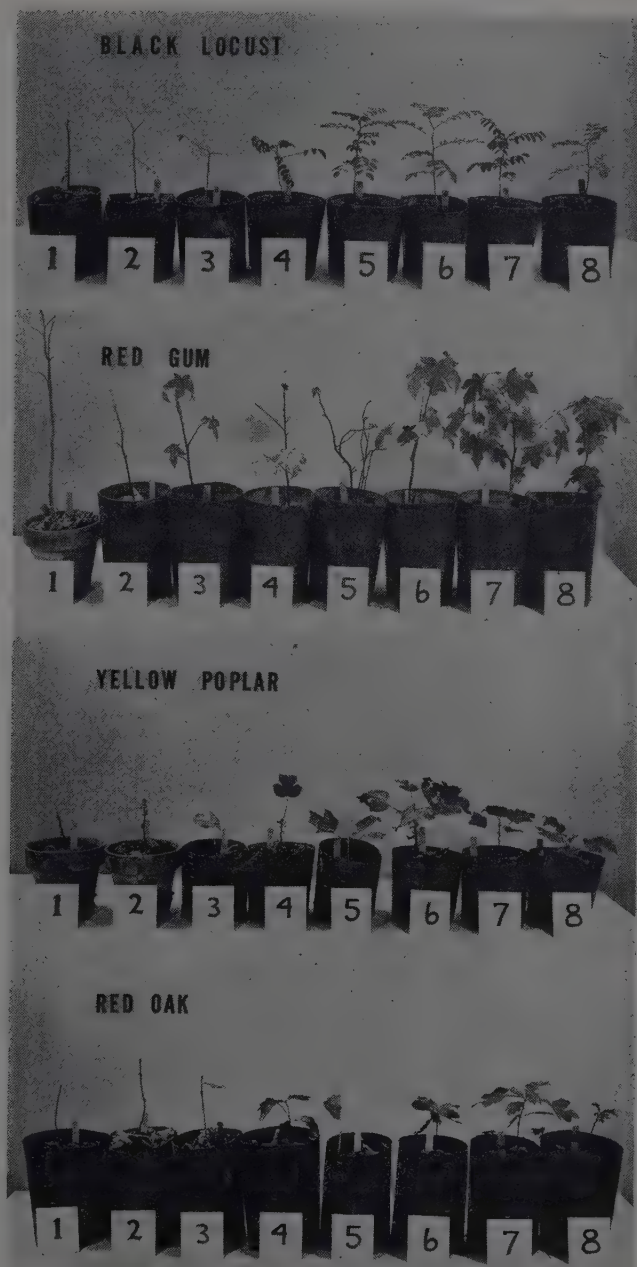
FIGURE 2. Appearance of the average plants at the termination of the experiment. Photoperiods: **1**. 0; **2**. ¼–hr.; **3**. ½–hr.; **4**. 1–hr.; **5**. 2–hr.; **6**. 4–hr.; **7**. 15–hr.; and **8**. 24–hr.

SUMMARY

1.   Scotch pine (Riga) trees planted in 1952 were covered with transparent, black, blue, or red polyethylene bags to observe the effects of light quality on winter chlorosis.

2.   Transparent, black, and blue polyethylene bags had no apparent effect upon the prevention of winter chlorosis.

3.   Red colored polyethylene bags prevented the onset and further development of winter chlorosis.

4.   Further work is planned to test the effect of light intensity as opposed to light quality.

DISCUSSION

DENNIS RICHARDSON (*University of Aberdeen, Scotland*):   In your experiment demonstrating that chlorosis in Scots pine trees can be arrested by covering them with red plastic, is it possible to separate the effect of red light *per se* and that if a reduction in light intensity is due to the cover?   (Observation of Dr. Richardson in the experiment relating abscission to very short [less than 4 hours] photoperiods).   It would be useful as a follow-up to this very interesting experiment to attempt to separate what have been described as, respectively, photo-energetic and photo-stimulative reaction, *i.e.*, in this case, to find out whether leaf abscission results from a reduction in the duration of exposure to light (or in truly "photoperiodic" responses).   This could be done by giving the same total amount of light energy spread over periods of, say, 4 hours and 15 hours.

JOHN HACSKAYLO: At the present time, no; however, we plan to run a more extensive experiment this fall and evaluate the effects of shading as well as color by using burlap.

HENRY G. GERHOLD (*Penn. State University*):   What wave lengths of light are transmitted by the red and blue plastics which you used?

JOHN HACSKAYLO: At present we do not know, but plan to have the transmission of light quality analyzed.

HENRY G. GERHOLD: Did you try other plastics besides polyethylene?

JOHN HACSKAYLO: No.

HENRY G. GERHOLD: Between what dates were the trees shaded, and how long thereafter did they retain their green color (trees covered by red plastic)?

JOHN HACSKAYLO: The trees were covered with the polyethylene bags on September 15, October 15, and November 15, 1956.   All of the bags were removed on December 15, 1956 with the exception of the September 15 series which were removed on November 15, 1956.

An Introduction to Reactor Physics.   *D. J. Littler* and *J. F. Raffle*.   McGraw-Hill Book Co. New York, 1st edition Oct. 1955.   196 pp. $4.50; 2nd revised edition Jan. 1957, 208 pp.

The first three chapters present a brief descriptive review of atoms, nuclei and radioactivity. The subsequent two chapters record the various equations associated with fission and neutron interactions.   Derivations are frequently omitted.   However, derivations are nicely present in the chapter on diffusion and would be welcomed by those not too well versed in the kinetic theory of gases.   The differential equations are set up and worked out in most instances.   Also, lattice constants and pile kinetics are well done.   The latter chapters on operation and construction of detection are too brief to be helpful to those other than the uninitiated in the field.   A chapter is devoted to the introduction to the very extensive subject of radiation damage.   Four appendices are included in the second edition.   The second edition contains several additions and considerable rearrangement of material.   No problems are included at the end of each chapter, however, several illustrative examples are worked out throughout the text.

                                                                                    M. L. POOL

THE MATING ACTIVITIES OF THE ANT
MYRMICA AMERICANA WEBER

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INTRODUCTION

Myrmica americana Weber is a frequent inhabitant of lawns as well as open pastures and undisturbed fields and meadows in the northern parts of middlewestern United States. Its nests are commonly formed of soil chambers at the roots of grasses. The number of chambers to a nest and the depth of the nests is variable, but there is a general uniformity of construction such as is also present in soil nests of other species of *Myrmica* in this region (see Talbot, 1945a, for the description of soil nests of *Myrmica emeryana* Forel). Surface chambers formed of bits of plant debris at the bases of grass clumps are common, especially in late summer. Such chambers function primarily in speeding brood development, but they are secondarily used to house the mature alates at the mating season.

Alates of *americana* begin to appear in nests in the southeastern Michigan—northwestern Ohio area about the latter part of July, and may usually be found in nests during August and September. The earliest record of mature alates in nests in this region is July 26 for a nest in Ann Arbor, Michigan in 1955. The latest record for this same area is October 15, also for a nest in Ann Arbor in 1955. However, mating observations presented below indicate that alates may be present in some nests for several days past this latter date.

The mating flights of this ant were first noted on September 15, 1955 from a nest on the University of Michigan campus, Ann Arbor. Subsequently, six more flights were observed from this and one other nest in Ann Arbor during September and October 1955. An additional flight was seen there on September 29, 1956. Flights from five nests on the campus of Bowling Green State University, Bowling Green, Ohio, were observed on 22 days between September 11 and October 18, 1956.

None of the nests under study were examined to determine the populations of the colonies because this would interfere with the normal flight activity. However, estimates of alate production per colony may be based upon the number of alates seen in flight. On this basis we believe that the most populous colony produced about 1000 alates, while the colony with the most sparse flights produced probably 100–150 alates during 1956. The ratio in each colony was usually two or three males to one female; however, there were about five males per female in the most populous colony. One small colony apparently produced only females.

CLIMATIC CONDITIONS

The conditions under which flights occurred were similar in the two localities; the observations obtained in Bowling Green in 1956 have been summarized in table 1. Flights of *americana* took place in late summer and early fall. The earliest seen were those of September 11, 1956 in Bowling Green. Because of the presence of many dead males in spider webs near the nests, it is presumed that flights had taken place earlier. Most of the alates apparently flew during September, but some were flying as late as October 18. Flights started as early as 9:30 A.M. and occurred as late as 6:30 P.M., but the period of greatest activity was from 12:30 P.M. to 4:30 P.M. The early flights all took place during cool weather in October, and the late afternoon flights all occurred during warm weather in the early part of September (fig. 1).

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Air temperature approximately six inches above the surface varied from 64° F to 88° F at the time of flights. Warmer temperatures were required for flights during the early part of the mating season than in October. There seemed to have been no direct influence of a maximal temperature within the time of study. The cool weather of early October apparently prolonged the duration of the flight season. A few more warm days in early October might have resulted in all alates flying much sooner.

Direct sunlight appeared to play an important role in the occurrence of flights early in the mating period. When temperatures were favorable, flights were often
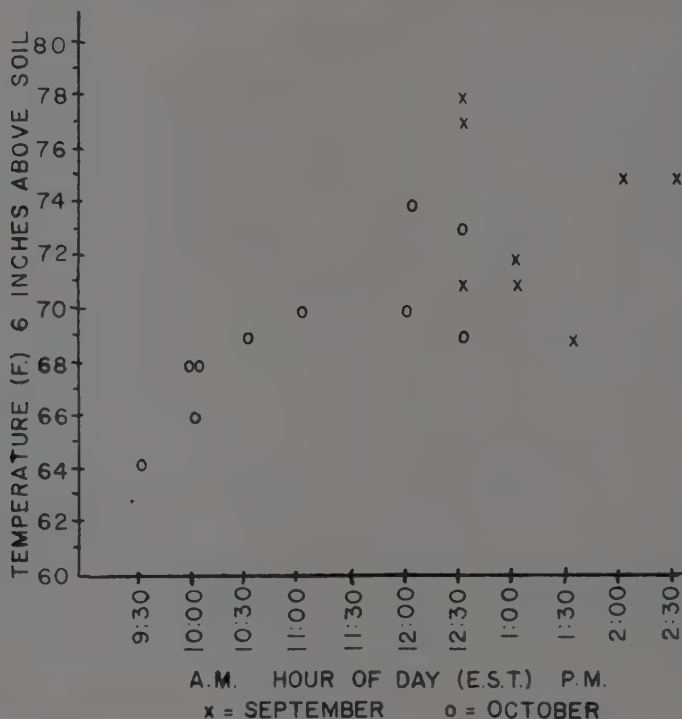
FIGURE 1. Correlation of temperature and hour at which flights of *Myrmica americana* Weber began in Bowling Green, Ohio, 1956. During the warm days of September flights occurred after noon and at temperatures of 69°F or higher. During the cooler weather of the first half of October the alates left the nests much earlier in the day and at considerably cooler temperatures. The presence of direct sunlight on the nest surface affected the time of flight during September, but this factor has not been considered in this figure.

large and continuous on cloudy days; on partly cloudy to clear days they were discontinuous, taking place when the nest sites were shaded, and ceasing (with the alates often returning to the nest) when sunlight covered the area. However, from the last week of September until the flights ended, mating flights seemed to be independent of light conditions.

Flights were most frequent on days that were calm or had only slight breezes

Alates appeared not to come out of nests on days of moderate to high winds. Except for a few rainy periods, moderate humidities prevailed during the mating season.   With the exception of an absence of activity during rains, no noticeable correlation was found between flights and humidity.

MATING BEHAVIOR

The amount and kind of mating activity varied considerably according to the favorableness of all weather conditions, with the largest flights occuring on warm, calm, cloudy afternoons in mid-September.   On such occasions flights were usually observed from all nests in the study areas.

Many of the flights in September took place under optimum climatic conditions, and the number of alates participating from a single nest was generally 30 or more. However, in October, with a few exceptions on very warm days, the flights were small (10 or less alates) and sporadic.   Most nests that were under observation had flights on those days in September during which conditions were optimal (see Table 1).   In the case of three nests all alates had left the nests by the end of September, but sparse flights continued from the other two nests until October 18.

TABLE 1

Conditions under which mating flights of Myrmica americana *took place in Bowling Green, Ohio, 1956*

	Date	Time	Temperature	Light	Humidity	Wind
Range of Observed Conditions	September 11 to October 18	9:30 A.M. to 6:30 P.M.	64°F to 88°F	Broad Sunlight to Dense Shade	30% to 80%	Calm to Slight Breezes
Optimum Conditions	September	12:30 P.M. to 4:30 P.M.	72°F to 80°F	Shaded from Direct Sunlight	45% to 60%	Calm

Apparently, all alates had left the nests by then, for no others were found later, although workers were seen on several occasions.

The larger flights were very noticeable, the smaller ones inconspicuous.   In all flights the alates flew singly; there were no mass emergences.   No swarms were noted; however, on days of heavy flights there would often be so many alates leaving the nests and the surface that the air a few feet above the ground would seem to be filled with swarming ants.

Early in the flight period there was considerable pre-flight activity.   The alates left the nest entrances and crawled about on the ground surface and on stems and leaves for some time before actually flying.   Much of this behavior seemed to be directed toward finding the proper site from which to fly.   Late in the fall, when temperatures were cooler, the alates spent less time in choosing such a site, and often flew from the ground surface.

The alates preferred to fly from some object that was raised above the surface. Because of its great abundance in the study areas, grass provided most of the promentories for these ants. Prior to becoming airborne the alates would hold tightly to the end of a blade of grass or some other object with the hind and middle pairs of legs, and would flutter their wings several times.   Then, releasing their grip on the object, they would rise into the air.   Alates flew in all directions and were seen to fly to heights of 40 feet or more before being lost to view.

Copulation was observed to take place on the surface and in the air.   Mating probably also took place within the nests for shed wings were found in nests, and

on several occasions dealate females were seen to crawl out of nest entrances and hide themselves in and under debris at distances of 3 to 17 feet from the nests. The amount of mating that took place within the nest is unknown. Copulation was frequently observed on the surface, and was seen to take place between presumed members of the same colony. Aerial copulation was observed on few occasions, usually on days of heavy flights. Pairs of alates which had mated in air would fall to the ground together and separate shortly. Some males were seen to copulate more than once on the ground, but no females were observed mating with two different males.

On the ground the males seemed able to recognize other ants only within distances of one to two inches. Males appeared to be just as excited when they encountered other males as when they met females. On several occasions males were seen to mount other males, but they usually separated quickly. Apparently visual recognition was rather ineffective, and recognition was due largely to odors or faint sounds, or both.

During copulation the male assumes a position dorsal to the female, holding on to the posterior portion of her thorax and to her gaster with his legs. When mating takes place on the surface, the wings of the female are held at the normal resting position, *i.e.*, horizontally over the back. Pairs were observed *in copula* on the surface for periods of 30 to 60 seconds. Those pairs that dropped to the ground after meeting in the air usually retained their union for no more than 30 seconds.

After copulation, the males would either fly off or crawl about on the surface in order to find other females. The latter, after copulation, would sometimes take flight, but in most cases would quickly cast off their wings. These newly dealated females would then seek places in which to start new colonies, generally under objects such as leaves, stones, pieces of wood, etc.

Late in the day, therefore, the mass of alates in the vicinity of a nest was composed largely of males. At the end of a day's flight some males and alate females were seen to return to the nest, but it was not possible to determine whether any of these had actually taken flight, or whether any had mated. Later in the evening other males could be found hiding in the vegetation. These males would reappear in the vicinity of the nest the next day shortly before the alates were to emerge from the nest. Thus, an abundance of males was maintained for the breeding population.

COMPARISON WITH OTHER MYRMICAS

The only other North American species of *Myrmica* for which detailed observations on mating activities have been published is *Myrmica emeryana* Forel. Talbot (1945b) studied the flights of *emeryana* from nests in a lawn in Tiffin, Ohio (approximately 30 miles southeast of Bowling Green), and found that the flights took place in mid-July from 6:00 A.M. to 8:00 A.M. at temperatures of 64° F to 74° F. None of these conditions correlates well with the conditions under which the flights of *americana* were observed.

However, certain aspects of the mating behavior of these two species are comparable. The size of the flights is small, usually less than 100 alates per colony on a flight day. Alates of both species apparently take flight singly and at random. In addition, their pre-flight behavior is similar in that they spend considerable time moving over the surface and vegetation searching for suitable sites from which to fly.

LITERATURE CITED

Talbot, Mary. 1945a. Population studies of the ant *Myrmica schencki* ssp. *emeryana* Forel. Ann. Ent. Soc. Amer. 38(3): 365–372.
— —. 1945b. A comparison of the flights of four species of ants. Amer. Midl. Nat. 34(2): 504–510.

RADIOACTIVITY AS A BASIS FOR CORRELATION
OF GLACIAL DEPOSITS IN OHIO[1]

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Robert Moxham, staff geologist of the Geophysics Branch, U. S. Geological Survey, recently informed the writer that glacial deposits of Wisconsin and Illinoian ages in Ohio were noticeably different in their radioactivities as indicated by a scintillation counter. This observation led to an investigation of glacial deposits in northeastern and east-central Ohio to determine whether radioactivity can furnish a basis for correlating glacial deposits of various ages.

Deposits of the Grand River Lobe were investigated in Trumbull, Columbiana, Geauga, Portage, Lake, and Cuyahoga Counties in northeastern Ohio. Deposits of the Scioto Lobe were investigated in Licking County in east-central Ohio. The deposits in northeastern Ohio were mapped and dated by White (1951a, p. 967–977; 1951b, p. 1489; 1953, p. 37); the deposits in Licking County were mapped and dated by Mr. George D. Dove of the U.S. Geological Survey (manuscript in preparation). Messrs. White and Dove mapped the glacial deposits in their respective areas as part of the Statewide program of ground-water investigations being made by the U.S. Geological Survey in co-operation with the Division of Water, Ohio Department of Natural Resources. The cooperation and field assistance of Dr. White and Mr. Dove are gratefully acknowledged.

EQUIPMENT AND FIELD METHODS

Two instruments were used to determine the radioactivity of the glacial deposits; a scintillation counter and a Geiger-Müller counter. The scintillation counter measures gamma radiation by means of a dense sodium iodide crystal which intercepts practically every gamma ray passing into it. The crystal is coupled to a photomultiplier tube that transmits the impulses to a meter which indicates the radiation intensity in milliroentgens per hour. The reading is not quantitative unless the instrument is calibrated. In this investigation the scintillation counter was not calibrated and the readings are merely relative measures of radiation intensity. The Geiger-Müller counter employs a gas-filled tube which reacts to about 1 percent of the gamma rays that penetrate it. The Geiger-Müller counter used in this investigation has two devices for indicating radioactivity: one is a meter that indicates intensity in milliroentgens per hour, useful only for sources radiating strongly enough to give a steady reading; the other is a scaler computer that counts the number of pulses in the Geiger-Müller tube. The number of counts per minute can then be used to obtain a near measure of true radioactivity with a calibration chart made for this particular instrument. This calibration chart is a curve obtained by plotting known radioactive intensities against counts per minute registered by the instrument when exposed to various samples of known intensities. The Geiger-Müller counter is sensitive to gamma and beta rays, the scintillation counter only to gamma rays. However, beta rays have low penetrating power and probably contributed little to the readings from the glacial deposits. The scintillation counter records many times more gamma rays from the same source as the Geiger-Müller counter, and, because it averages many more pulses per minute, gives a steadier reading. Both instruments normally indicate a small intensity (background) due to cosmic rays and internal contamination.

An important factor in radiation studies is mass effect, which means simply that the mass of the sample has an influence on its radiation intensity. Thus, a radioactive deposit in place will give a higher reading than a hand sample of the same material. Grain size also has an effect on radiation, and specimens ground to pea-gravel size and to powder will give successively higher readings than a specimen of the same volume left whole. In this investigation it was found that a typical exposure of till might give several different readings depending on the presence of gravelly or sandy layers. In an effort to obtain an average measure of radioactivity several readings were made at different places in such material.

The procedure found to be most satisfactory was to auger holes into the material to be tested, the holes being either of the size of the Geiger-Müller probe, about an inch in diameter and a foot deep, or that of the scintillation-counter barrel, about 3 inches in diameter and 6 inches deep. Placing the probes in the holes shielded them from most stray radiation, so that the instruments gave truer readings. At most of the test sites, the hole made for the scintillation counter was used for the Geiger-Müller probe also, to permit the tests to be made more rapidly. In northeastern Ohio, the probes were placed in the exposed material at various points where changes in composition were observed. In Licking County the readings were made at the contact of the A and B horizons in the soil, at the contact of the B and C horizons, and as low as possible in the C horizon, usually about 6 feet below the top of the exposure. Readings in till were not significantly different between soil zones, except where the different zones coincided with changes in composition. Leaching showed no apparent effect on radiation, nor did oxidation.

RESULTS AND DISCUSSION

Summarized in table 1 are the results of the tests in terms of ranges and median values of the observed readings. As shown in the table, there is, with one exception, a general trend from higher readings in younger deposits to lower readings in the older deposits. The trend is more pronounced in northeastern Ohio than in Licking County. In the Licking County readings little difference is shown between the various Wisconsin substages. The ranges of the readings from deposits in Licking County also are smaller than the ranges of the readings from deposits of corresponding ages in northeastern Ohio, perhaps because fewer tests were made in Licking County. The Licking County readings are, however, comparable in intensity to those made in northeastern Ohio.

Although most of the Geiger-Müller readings are in agreement with the scintillation-counter readings, the instruments do not always substantiate each other, especially in readings from coarse material. Poor correlation between readings may result from differences in grain size, which may account also for the wide ranges of the readings from deposits of the same age. Contrary to the general trend is the median Geiger-Müller reading from Illinoian deposits in northeastern Ohio, which is as high as the median of late Wisconsin deposits.

CONCLUSIONS

The principal advantage, thus far, of determining radioactivities of glacial deposits seems to be as an aid in making general distinction between deposits of pre-Illinoian(?) and Illinoian ages, and between deposits of Illinoian and Wisconsin age. General field use of the method for simple and accurate determinations of the age of glacial deposits does not appear imminent. A major disadvantage of the method is that the instruments are delicate and must be handled carefully. Moreover, they are very expensive. It is unfortunate that one instrument used in this investigation was not calibrated, for this will prevent comparison of the readings with future readings of other instruments. Obviously, more use must be made of the method before its true value is known. A laboratory investigation

TABLE 1

READINGS FROM GLACIAL DEPOSITS OF VARIOUS AGES IN OHIO

Age		Description	Range & median[1] of readings (line shows approx. trend) Geiger counter (cpm)[5]	Scintillator (mr/h)[5]
NORTHEASTERN OHIO				
Latest Cary[2]	43[3]	Silty pebbly till, some sand		
Late Cary[4]	16	Compact clay till, silty		
Early Cary	13	Sandy till with gravel		
Tazewell	14	Coarse stony, till, sandy		
Illinoian	6	Clayey till; gravel fresh & weathered		
Pre-Illinoian (?)	4	Colluviated, weathered outwash ?	40 60 80	.020 .030 .040
EAST-CENTRAL OHIO				
Late Wisconsin (Middle Cary?)	7	Clayey, fine shaley particles, sandy		
Middle Wisconsin (Early Cary?)	7	Shaley till, sandy		
Early Wisconsin (Tazewell)	3	Sandy till, coarser than late Wisconsin		
Illinoian	7	Sandy, oxidized till, coarser than Wisconsin	40 60 80	.020 .030 .040

1/ ⌐ median of all readings from a particular age.

2/ Painesville member, Lake Escarpment moraines.

3/ Number of sites sampled.

4/ Defiance moraine and related till.

5/ (cpm) counts per minute; (mr/h) milliroentgens per hour.

of samples of known ages in various quantities and grain sizes might result in a more reliable field technique. A radioactivity investigation in which a large number of tests were made possibly could serve as a basis for correlation of gamma-ray logs of wells and point the way to an important new technique of subsurface mapping.

REFERENCES

White, G. W. 1951a. Illinoian and Wisconsin drift in the southern part of the Grand River Lobe. Geol. Soc. America Bull. 62: 967–977.
———. 1951b. Pleistocene stratigraphy in northeastern Ohio (Abs.). Geol. Soc. America Bull. 62: 1489.
———, in Winslow, J. D., G. W. White, and E. E. Webber. 1953. The water resources of Cuyahoga County, Ohio. Ohio Dept. Nat. Res., Div. Water Bull. 26, pl. 26.

Biochemical Individuality. *Roger J. Williams.* John Wiley and Sons, New York. 1957. 214 pp. 17 figures, 17 tables. $5.75.

This book is a compilation of data to show that every genetically distinct individual is biochemically different from every other individual with respect to the amounts of all chemical constituents so far tested, excretion patterns in the urine and in nutritional requirements. The latter embodies what the author calls the "genetotrophic concept." The differences between the few persons tested have often been as great as ten fold or more. The maximum requirement of one person may be only a tenth as much as the minimal requirement for the same substance in another person. Disease is regarded as the failure in nutritional intake to meet the optimal needs of the individual for a specific chemical compound. Nutritional science has solved the etiologies of such diseases as scurvy and pellagra, but has failed to explore the probability that nutritional deficiencies are the basis of diseases, the causes of which are still obscure.

About one seventh of the text is devoted to anatomical variations (*e.g.*, difference in branching of nerves, ducts, blood vessels), regarded as genetically produced. No evidence is offered in support of this contention such as similar or identical patterns being found in identical twins or in members of the same inbred strain of animals. The reviewer is an ardent believer in the importance of heredity, but would suggest that this chapter is out of place in a text on biochemical variations, and that the assumption that because there is variation, it must of necessity be genetic, may not be justified.

Finally the author injects a totally unwarranted and extraneous piece of propaganda into his text when he states that if human beings are as highly individualistic as the data indicate, "It is clear that the patient—personal physician relationship is extremely valuable, and any system undermining it should be shunned." He further states that only if people are replicas of each other can they best be looked after by a government established "Health-mill," but that the data on biochemical individuality point in the opposite direction. The reviewer would point out that yellow fever, small-pox, diphteria, malaria, etc., were successfully eliminated by treating people as if they were replicas of each other so that the health mill has ground out some rather valuable results. Furthermore, the reviewer is not aware that the patient selects his physician because of smilarity in blood groups, excretion of amino acids, or vitamin requirements. The much discussed "personal" relationship between patient and doctor usually consists of an intimate two hour acquaintance with the magazines in the waiting room, and a too often cursory examination of ten minutes or less in the inner sanctum.

Nevertheless, this is excellent source material for persons interested in biochemical variations; but the reviewer wonders just how *practical* the author's *practical applications* are. If every patient must be investigated biochemically for all of the constituents encountered in the human body, the time and cost of such a program would be prohibitive.

MADGE T. MACKLIN, M. D.

Control of Nuclear Reactors and Power Plants. *M A. Schultz.* McGraw-Hill. New York. 1955. 313 pp. $7.50.

The basic nuclear physics of nuclear reactors are not emphasized in this book. The control problems are extensively and thoroughly considered. Frequent use is made of block diagrams. The book is most suitable for engineers who understand servomechanisms, electronics and mathematics. The subject matter is very practical, such as starup control, power operation control, and shutdown control. A chapter is devoted to simulators. A list of problems is included for ten of the eleven chapters.

M. L. POOL

INDEX TO VOLUME 57